

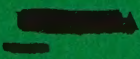
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SVENSKA VÄXTGEOGRAFISKA SÄLLSKAPET

Hans Olsson

Studies on
South Swedish sand vegetation

Lund
 1974

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The vegetation on sand in South Sweden, is distributed within the Scandinavian outlier of the Nemoral zone. From the 16th century documents record the sand shifting. Later many sites were planted with marram grass and pine.

Of the flora the genus *Cladonia* is extensively treated. The phytosociological investigation, agreeing with the Braun-Blanquet system, mainly stresses the floristic composition, in certain cases with stronger consideration of the physiognomy. 36 plant communities, many new or differently conceived, are arranged in 18 classes. The synthetic description of the vegetation deals with classification, structure, development, ecological remarks, distribution and sociological relationships. Vegetational changes and development from immature to mature soils during different processes have been investigated.

A number of climate-phytomorphous and hydromorphous soils are treated. A halo-nitrosere contains two series. A xerosere is split into a maritime dune subsere, a subsere of the sand affected by man and a subsere on inland glaci-fluvial sand. A hygrosere consists of a eutrophic subsere and an oligotrophic subsere with two series: one zonation on the west coast and one mosaic complex at Sandhammaren (Baltic coast).

The ecological relationships between Sandhammaren and Tönnersa (west coast) are particularly compared. The variation in horizontal and vertical distribution of soil parameters such as water content, loss on ignition, pH and various nutrients is studied in relation to investigated vegetation units and gradients (seres). In the plant cover a quotient metals/total elements was higher at Tönnersa than at Sandhammaren.

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Preface

The provinces of Halland and Scania are rich in sandy fields and sand dunes, particularly along the coasts. Most localities are non-calcareous and acid, except Vitemölla. Most of the coastal sand is aeolian, but inland there are glacifluvial sands too. Early records of the dune vegetation are fragmentary, though the sands have interested man since the time of Linné. Parallel to natural vegetational changes human activity has transformed the landscape during the last centuries. Today very distinct floristic borders can be seen within the investigation area. My intention with this work is to study the differences of the vegetation in time and space. The first part is a regional study of the vegetation in South Sweden. The chief aim is to present a descriptive account of the composition of the vegetation, its classification and distribution, and also to describe the soil types. At the start of this work, in 1965, the study was restricted to the maritime sands. Later the inland sands were included too. The last chapter deals with chemical and physical problems.

The investigation was started in 1965 at the Department of Plant Ecology, University of Lund, and is still in progress. The main field work was done

in the second half of the 1960's. For valuable advice during the course of this study I am greatly indebted to Professor Nils Malmer, head of the Department of Plant Ecology. Dr Åke Persson, Lund, has given me much help with the treatment of the phytosociological analysis. Allan Nicklasson, fil.lic., Växjö, has identified some bryophytes. Bo Wallén, fil.mag., Lund, working on the energy relations at Sandhammaren, has in recent years assisted me in the field work. The drawings have been made by Mimmi Varga and the language is revised by Gail Åkerman.

For valuable discussions of the manuscript I am grateful to Professor Tyge Böcher, Copenhagen, Dr Richard Clymo, London, Göran Mattiasson, fil.lic., Lund and Mr Åke Rühling, Lund. Furthermore I should like to thank Gunnel Sjörs, technical editor of the *Acta Phytogeographica Suecica*, for help and advice with the publication.

Lund March 1974

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The investigation area

Dune areas and sandy fields in South Sweden are situated west and south of the Caledonian Rocks, located inland and in coastal areas. The western dunes can be regarded as the northern offshoots of the phytogeographically extensive Atlantic dune system, the eastern ones are representatives of a Baltic system. The inland dunes are similar to corresponding dunes on the Continent. The investigation area is illustrated on a survey map (Fig. 1), on a map showing the localities studied (Fig. 2), and on a map placed in a hypothetically phytogeographical quadrant system (Fig. 3).

The investigated area includes parts of the provinces of Halland and Scania. In a wider perspective the provinces of Blekinge, Småland and Öland also belong to South Sweden, but the sands there are not treated in this work. Of course the sands occupy only a small part of the whole area. Much of the

coast of South Halland and Scania consists of sand. The inland sands are scattered. The Vomb sands in the middle of Scania and the dune field just north of the lake of Bolmen in the province of Småland are examples. Though the selected localities differ in morphology, geology, climate, cultivation, vegetation and flora, they are representative of many similar localities in the investigation area and together they allow a phytogeographical and ecological synthesis of the whole area to be made.

The areas investigated are:

Haverdal (Ha): around the bay Haverdalsbukten, near the sea shore, 1.7 km inland.

Tönnersa (Tö): around the bay Laholmsbukten, near the sea shore, S part near the river Lagan, N part near the river Genevadsån, 3 km inland.

Ängelholm (Äh): around the bay of Skälderviken, near the sea shore towards Vegeholm, also inland.

Falsterbo (Fa): the peninsula of Falsterbo, the south spit.

Sandhammaren (Sh): the foreland of Sandhammaren, between the lighthouse and the Kåsebergaåsen-esker.

Vitemölla (Vm): around the bay of Åhusbukten, S part near the seashore.

Furuboda (Fb): around the bay of Åhusbukten, middle part near the seashore.

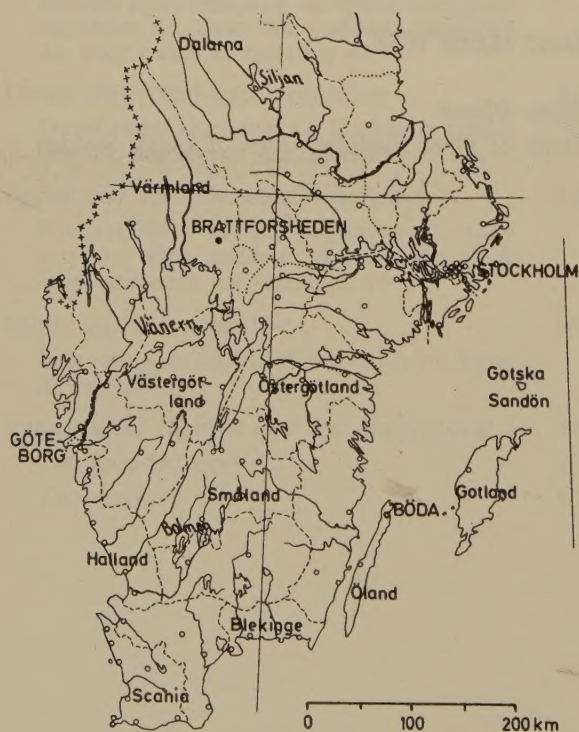


Fig. 1. South part of Sweden.

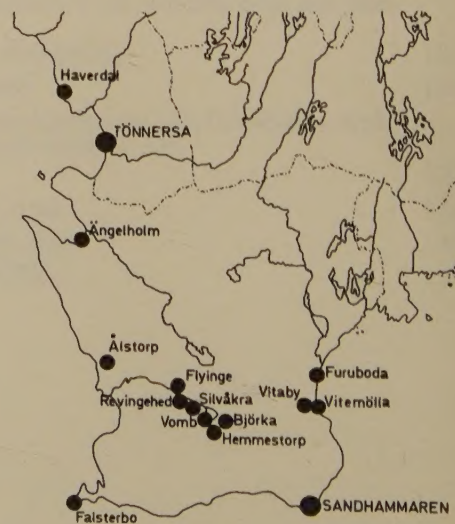


Fig. 2. The investigation area.

Ålstorp: between the village of Saxtorp and that of Löddeköpinge, West Scania.

Flyinge: near the village of Flyinge, NW part of the Vomb plain, central Scania.

Revingehed: near the military base training camp, NW part of the Vomb plain, central Scania.

Silvåkra: near the river Klingaälvsån, central part of the Vomb plain, central Scania.

Vomb: near the village of Vomb, central part of the Vomb plain, central Scania.

Björka: near the river Björkaån, NE part of the Vomb plain, central Scania.

Hemmestorp: near the small village of Hemmestorp, S part of the Vomb plain, central Scania.

Vitaby: between the village of Vitemölla and that of Vitaby, East Scania.

The landscape in glacial time

Many dune areas, especially along the coasts date from late glacial time. The inland dunes, formed during the late-glacial period or even early postglacial time, are glaci-fluvial in origin with homogeneous sand (Lundqvist, J. 1963 pp. 34-35). According to Hörner (1926) the necessary requirements for the formation of dunes were at hand, as the melting water of the inland ice filled up a great number of regions with sand, both valleys and other places.

Scandinavian dunes were formed in front of the retreating ice. Often the sand was moved west or south (Lundquist, G. 1920). Large sand bars were deposited in or near lakes or bays of the sea at that time, for example at Bolmen in the province of Småland and at Siljan in the province of Dalarna (Fig. 1). The main sand movement probably ceased early, for the latest parts about 4-5000 years ago. Lundquist, G. (op.cit.) has shown that sands from the province of Västergötland have been covered by vegetation since early subboreal time. The inland dunes are concentrated in the deltas, in front of the inland ice, where the plain was open and unprotected from winds and there was little vegetation. Nowadays the inland sands are covered by pine

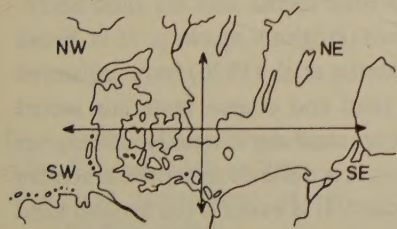


Fig. 3. South Sweden in a hypothetical quadrant system.

forests. The extent of aeolian sand in Sweden can be seen in Fig. 4, on the Continent in Fig. 5.

Topography, geology

Sand sediments were deposited in ice lakes (Vomb plain), along coasts or on sandy fields. These soils are easily eroded by winds forming dune landscapes. The small resistance against erosion by the sea is thus a cause of the soft coasts in Scania. The Vomb plain, compared with other inland sands rather small



Fig. 4. Distribution of aeolian sand in Sweden (from Atlas över Sverige 1953-71).

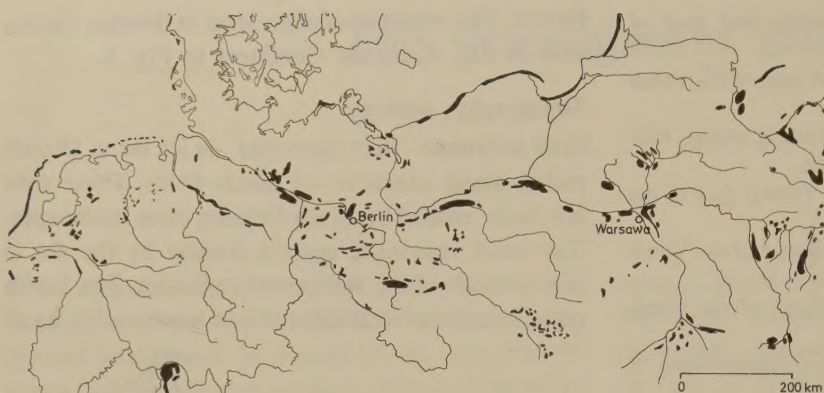


Fig. 5. Sands south and west of the Baltic (from Högbom 1923 pp. 178-179).

and more heterogeneous in the soil, is composed of sandy deposits (Saxtorp) or sand sediments with stratified clays (Vomb) indicating complicated ice conditions. The Vomb plain has a prolongation along the river Kävlingeån to West Scania, to the hills of Brösarp in East Scania and to the lakes near the village of Sövde in the South.

Soils and soil regions are given in Table 1.

With few exceptions all recent dunes are connected with seashores, where sufficient quantities of sand are supplied by the wave action. Inland dunes independent of shore lines have, in several cases, moved towards the shore under the influence of land winds. Genetically these dunes are inland dunes (Högbom 1923). The dune system at Brattforsheden (Fig. 1) in the province of Värmland (Hörner 1926 p. 96) consists of glaci-fluvial material transformed into gravel deposits and layers with aeolian sand preserved from the time of formation. Of interest are also the Bothnian Bay dunes probably formed from glaci-fluvial deposits.

The sands are composed of fine and coarse sand, acid and poor in minerals and often very well sorted. The grain size has no direct effect on the vegetation. Du Rietz, T. (1953) has studied the mineral composition, size and form of the sand grains. There is only a little increase in the quartz content in Bothnian seashore sand compared with that of the southern Baltic: SiO_2 increases from 70-75 % to about 95 % and Al_2O_3 decreases from 15 % to 5 %. To some extent this could be explained by the fact that the Cambrian sandstone in SE Scania is very rich in quartz. In dune sand from the province of Halland and in the Vomb plain the SiO_2 content is 80-90 %.

In general the aeolian sand is uniform, sometimes only one grain size. The sand consists of quartz, feldspars and mica and corresponds to the composition of a gneiss rock. Yellow sand is rich in quartz,

brown in feldspars and white in shell fragments. The differences in colour are due to precipitated iron compounds, a layer of hydrated iron round the grains. Heavy grains with much iron can be collected in ripple marks on the beach. Dark sand on the sea shore is often a result of the reduction of sulphates to sulphides in the presence of organic matter. In Sweden the quantities of shell fragments take no or very little part in the dune formation. The medium size of the sand is 0.2-0.6 mm, more rounded grains in southernmost Sweden compared with northern parts. Davidsson (1963, 1964) has made petrographic analyses. At Sandhammaren there is good stratification regarding size, density and form. Marine gravels can be seen at Haverdal inside the outer dunes, at Sandhammaren behind the dune landscape, in the beach ridges at Järarna (see Moberg 1895).

The aeolian sand, dominated by quartz, is in general, as in the inland, non-calcareous with little feldspars, but compared with desert dunes and maritime dunes, it is not pure quartz. Instead the minerals have been mixed. A certain grain size is left in the dunes while finer materials are transported. Coarse grains can be seen in deflations. There is a genetical correlation between aeolian sand and aeolian mo-clay. The latter is probably transported by winds, the former via saltation. Afterwards the two fractions have been united and the sand accretion could be stopped (Högbom op.cit. p. 161). From the Vomb plain Munthe et al. (1920) have registered both fine aeolian sand and coarse materials mixed with quartz, feldspars and dark weakly calcareous minerals. Sometimes it is difficult to separate aeolian sand from marine sand. It is easier if the aeolian sand has covered peat layers lying on marine sand, seen in some places in Halland (see Mohrén & Larsson, W. 1968 p. 86).

Table 1. Soils (area %) in soil regions (from Atlas över Sverige 1953-71).

area	bedrock	till	glacifluv. gravel	sand	clay	boulder clay	peat
Scanian clayey till	<1	<5	10	15	5	65	5
Vomb region	—	<5	25	45	5	10	15
Laholm region	10	15	<5	50	20	—	<5
Ängelholm clay, till and sand	—	15	<5	35	40	10	—
Kristianstad region	—	25	<5	35	10	—	10

Coastal types

The bays of Hanöbukten, 27.5 km in length, in East Scania, and that of Laholmsbukten, 32.5 km in length, in South Halland are fairly round, whereas the bay of Skälderviken is more elongated. Its shape is determined by the surrounding bedrock. Only at the inner parts does the soft shore line describe a part of a circle. The bays in the province of Halland, not only the bay of Laholmsbukten but also the smaller ones further to the north at Tylösand and Haverdal, are situated between rocks. The smooth sandy bays are replaced by an archipelago north of the town of Varberg. Earlier the southern parts of Halland also consisted of an archipelago (von Post 1933, Öster 1952, 1960). Rocks and islands can also be found on the northern part of the bay of Hanöbukten and further westwards in the province of Blekinge.

In the rather uniform coast of southernmost Scania there are two formations of special kind. The peninsula of Falsterbo, rather young, resulting from offshore bars connected with each other and with the earlier coast, is originated as a compound island of bay bars (Davidsson 1963). The foreland at Sandhammaren can be compared to a triangle, with one angle turned to the sea. Bay bars running in an easterly direction have been connected with an elevated northern area (Richter 1934-36, Davidsson op.cit.).

Radiation and temperature

Near the coasts there are more than 2000 sun hours a year and as a consequence the precipitation is low. There is a diurnal fluctuation of the wind during the summer, from the sea to land and reversely. An advective heat transport between land and sea takes place. The maritime zone reaches 30-40 km inland on the Swedish west coast, but along the Baltic coast it is not so pronounced. The Atlantic air dominates in the summer and in the autumn. A temperature gradient from the British Isles to the eastern Baltic (Fukarek 1961 p. 20) shows that the difference between the coldest and the warmest months increases (Fig. 6). The maritime influence is most pronounced in April. The delay in spring is greater at the Baltic coast compared with the west coast, whereas the autumn is warmer.

Normally the mean annual temperature is 7-8°C, for July 16-17°C and for January-February about 0°C. The yearly amplitude is 16-18°C (Atlas över Sverige 1953-71). The mean annual value for Halmstad 1966-70 is 6.8°C and for Ystad 7.3°C (SMHI). These values are slightly lower compared with the period 1901-30 (Table 2). The mild winters, rarely below zero, have a maritime character. Thus the frost period is very short, no frost at all from May 15 to September 15. The summer is long, 144 days with more than 10°C. In the sandy areas the

Fig. 6. Temperature gradients (after Fukarek 1961 p. 20).

— mean temperature of the warmest month
 mean temperature of the coldest month
 - - - - range of annual temperature

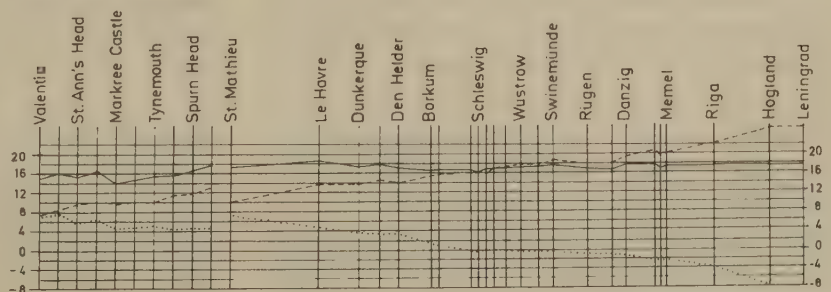


Table 2. Precipitation and temperature 1901-30 (From Bergsten 1947, 1952, Ardö 1957 p. 27).

locality	annual prec. mm	yearly mean temp. °C	temp. ampl. °C
Falsterbo	442	7.9	16.4
Ystad	563	7.5	16.1
Sandhammaren	588	—	—
Övedskloster	633	—	—
Kristianstad	550	7.5	17.3
Båstad	799	7.3	17.5
Halmstad	746	7.6	17.6
Tylön	560	—	—

local climate is important. The temperature can rise and fall rapidly, more on the sand surface than on grounds covered with vegetation. The conditions are very different on lee slopes compared with windward sides.

Precipitation, humidity, vegetation period

Precipitation varies more than temperature, though the annual precipitation is low. Maximum occurs in July-August, more pronounced at the west coast than at the Baltic. Often there is a secondary maximum in October-November. Fukarek (1961 p. 25) has estimated the degree of oceanity as the difference between the mean precipitation during April-September and October-March, which gives better relations between maritime and continental climate than only the annual precipitation. In Halland there is a sharp gradient from the coast (600 mm/year) to the South Swedish highlands (1000 mm/year). During 1966-70 (SMHI) the mean values from Ystad and Halmstad are 602 and 765 respectively. Snow comprises 15-20 % of the annual precipitation. In summer the clouds are few; in winter the mists are common. The precipitation during the vegetation period is about 150-200 mm in SE Scandia and 275 mm in coastal Halland (Atlas över Sverige op.cit.).

Hesselman (1932) has determined the humidity as de Martonne's index during the vegetation period. The coasts along South Sweden have a dry subarid climate, index about 30 (Atlas över Sverige 1953-71). The low humidity is a combined action of precipitation and temperature. Tamm, O. (1959) established the humidity index as a measure of the average run-off. The Tamm index gives a better idea about the tendency of podsolation. The mean value (13⁰⁰) 1966-70 (SMHI) is for Halmstad 78 and Ystad 77. The conditions just near the sea differ from those of the inland (see Sterner 1922 pp. 358-

359). The more precipitation and evaporation approach each other the weaker is the drainage and thus the leaching. The vegetation utilizes the precipitation during the vegetation period and to some extent soil water from late winter.

The vegetation period is about 240 days (>3°C) or according to Langlet (1937 p. 373) only 180 days (>6°C). The length of the vegetation period has fluctuated during the 20th century. The autumns have been milder and thus the period longer. Now when the length is decreasing, the temperature seems to be lower.

Winds, water level

A flow of low pressures in South Sweden is directed to the east or northeast. On the south side of the low the winds are stronger. The prevalent winds are strongest during the summer, higher for east than for west winds. The winds have little importance for the vegetation as a whole but can strongly influence the outer dunes. The wind components are of great importance for the marine exposure (Bergstedt 1931, Richter 1934-36, Ardö 1957, Davidsson 1963, 1964), especially the number of hard winds. According to Sandberg (1929) the mean direction during July-September is W 26.4 S and for the whole year W 46.3 S on the Swedish west coast. Gales (>24 m/sec) occur during November-January. The lightest winds appear during May-June. The autumn activity starts in August-September.

West winds dominate, at Sandhammaren about 60 % from SE-NW and 40 % from SE-NE during a 10-year-period. The gale in October 1967, 60-75 % from SW and only 0-1 % from NE (SMHI), is probably the most severe in South Sweden since 1902. At Furuboda on the bay of Hanöbukten there are both SW-W winds and sea winds in the outer parts. Changes in the water level depend on changes in the weather. The water rises if there is a low with landward winds and falls with pressure and seaward winds. In storms with eastern winds the water level can rise about one metre on the east coast. In South Sweden the tides have no influence on the water level.

The South Swedish sands in the literature

In the 18th century, the Linnean era, the economic attitude to the sands was quite clear, probably the first contributions to modern ecology in Sweden. The most important works are: Linné (1749), Hallen-

borg, C. (1750), Lidbeck, E.G. (1759), Cronberg (1762), Montin (1768), Retzius (1776), Lidbeck, A. (1795), Osbeck (1796). Of other works of special interest can be mentioned: Richardson (1752-53), Tidström (1756), Fischerström (1761), Montin (1766), Barchaeus (1773), Osbeck (1776).

In the 19th century pine cultures dominated the contents as in the following works: Bruzelius (1802), Odencrants (1817), Hallands Läns Hushållningssällsks Handl. 1820 & 1847, Christianstads Läns Kongl... Handl. 1823-38, Malmöhus Läns... Handl. 1817-1825, Bruhn (1862), Skogsstyrelsens... Skogsväsendet 1876-79, Lindbohm (1891), Noreen (1891), Vistelius (1891), Sylvan (1892). Also in the 20th century several researches are concerned with the afforestation: Hemberg (1904), Mellström (1914), af Petersens (1932), Betänkande... flygsandsfält i Hallands län (1936), Malmström (1939), Månsson (1960), Troedsson (1964).

Phytogeographical aspects and floristic notes of the vegetation have been given by many authors: Topografiska... Halmstads län 1847, von Post (1863), Theorin (1865), Areschoug (1866), Topografiska... Kristianstads län 1876, Neuman (1884), Erikson (1896), Nilsson, A. (1905), Norlind (1913), Sernander (1915, 1917, 1920, 1925), Turesson (1919), Sterner (1922, 1924), Sjöbeck (1923), Hård av Segerstad (1924, 1925), Gertz (1933, 1948), Weimarck (1940, 1947 a, 1950), Nordin (1941), Suneson (1942), Andersson, O. (1950 c), Hallenborg, T. (1956), Falk (1957), Selander (1957), Sjögren (1957), Gustavsson (1968), Nilsson, Ö. (1968). Studies of ecotypes and chromosome numbers can be found in Turesson (1922, 1925), Lövkvist (1962) and Kjellqvist (1964). The cryptogams have been investigated by Osbeck (1762), Waldheim (1947), Andersson, O. (1950 b), Du Rietz, G.E. (1952), Hasselrot (1953) and Olsson, H. (1972 b). Of the different floras can be mentioned: Osbeck (1788), Fries (1817-19), Areschoug (1881), Neuman & Ahlfvengren (1901), Weimarck (1963).

Plant sociology and ecology have been treated by Warming (1909), Holmgren (1921), Sterner (1922), Sernander (1925), Vallin (1925), Böcher (1943 a), Dahlbeck (1945), Andersson, O. & Waldheim (1946), Andersson (1950 a), Tüxen (1951), Bergholz & Holmquist (1955), Ardö (1957), Damman (1957), Gimingham (1962), Malmer et al. (1965), Nilsson, N.-G. (1966), Rasmusson & Rasmusson (1970),

Olsson, H. (1971) and Tyler et al. (1973). Vegetational changes have been registered by Wibek (1906), Erdtman (1952), Mattiasson (1970) and Olsson, H. (1972 a). Several maps with descriptions also point out the changes in the landscape: Söderlingh (1691, 1698), Kanter (1750), Kock (1765), Dahlbom (1777/78), Lindblom (1782), Brandberg (1819), Malmström (1936, 1937), Troedsson (op.cit.), Olsson, H. et al. (1971).

A survey of the sand vegetation is given by Pettersson (1965), who in particular emphasizes the changes brought about by man and domestic animals.

Several works are concentrated on nature conservancy: Naturskyddsföreningens... Haverdalsområdet (1937), Nordin (1938), Dahlbeck (1940), Glimberg (1955, 1964), Weimarck (1960), Malmer (1968 b), Andersson, E. & Nilsson, J. (1971), Larsson, A. (1971), Mattiasson (1971), Olsson, H. et al. (op.cit.), Ljungberg & Persson, Y. (1973).

The geological researches are comprehensive: Lindström (1880), Erdmann (1881), de Geer (1889), Holst (1895, 1902), Moberg (1895), Kurck (1917), Munthe et al. (1920), Nilsson, T. (1935), Du Rietz, T. (1953), Caldenius et al. (1966), Nilsson, K. (1966), Mohrén & Larsson, W. (1968). The geographical works are mainly concerned with the dynamic processes or the erosion problems: Palm (1919), Nelson (1923), Bergstedt (1931), von Post (1933), Richter (1934-36), Ardö (1950), Öster (1952, 1960), Jansson (1959), Behrens (1960), Améen (1962), Rasmusson (1962), Davidsson (1963, 1964), Mattsson (1964), Bergström (1968), Norrman (1971). Remarks on soil science are found in Schlichting (1954, 1955), Linnermark (1960, 1966), and Ekström (1961).

The following zoologists have investigated the sands: Ringdahl (1921), Agrell (1934), Ardö (1957), Almquist (1969). Archaeology and historical culture are also of importance for understanding the conditions of the recent vegetation: Söderberg (1903), Campbell (1928), Jönsson (1934), Olsson, A. (1940-45), Sjöbeck (1945), Löfström (1946), Hommerberg (1955), Strömberg (1971).

THE DUNES

The width of a coastal dune can increase as a result of moving landwards or moving seawards as a consequence of accumulation, seen at Sandhammaren.

The main part of the sand transport occurs near the ground. The result is vertically growing dunes. Wind furrows can change the direction of the transport. The height of the dunes depends on the height and density of the plant cover, the sand volume above the ground water table and the wind force. The vegetation accumulates the sand through the lee influence or protects the dunes from deflation. Irregularly supplied material involves a periodicity in the dune growth. The moisture on the ground surface is an important factor. The combined action of wind and water can have a negative effect on the dunes. As a rule the accumulative and positive transport occurs during spring and summer, the erosive and negative transport during autumn and winter. These two phases play an important role in the whole dune system and the life of biota (Ardö 1957 p. 28), as well as the size and direction of the dune migration.

In flat coast areas, where the supply of sand is enough, dunes will be formed inside the beach. The dunes are built up by sand eroded from the dry shore. The dune front can be eroded by surging waves. The sandy bays, on the western coast and Scanian east coast, are orientated perpendicular to the resultant of the wind-generated waves. The wind force can be divided into two components, one acting along the shores and the other, perpendicular one, is a measure of marine exposure. Changed wind regime disturbs the balance between accumulation and erosion and a new balance with a new resultant appears. Currents with a speed of 2.5 m/sec in the surface (Richter 1934-36 p. 30) form grooves outside the shore and often between several submarine bars, one just near the shore (Schou 1945 pp. 67-70). At high water level, developed beach ridges may be destroyed and moved landwards, at low water level seawards. The upper border of the beach is exposed to surging water. On the west coast the rivers debouch to the north. On the bay of Hanöbukten in East Scania the currents transport sandy materials from south to north.

The sand grains are transported rolling on the surface or via saltation (Bagnold 1965 pp. 19-20, 126-127). Ardö (1957 p.25) has found that the mean velocity for a wind with aeolic capacity is about 5 m/sec near the ground. In spring the grains attain a high velocity, sometimes resulting in a blasting effect, together with salt spray severe for the pines and thus with an erosive result. Strong winds erode along dune walls near wind furrows, if free from vegetation

contrasting sharply to surrounding dunes. The dune front near the sea, as at Haverdal and Tönnersa, may be exposed to destructive erosion. As a result of human activity small wounds can develop into large deflation scars.

On the beaches sometimes there are small half moon dunes, miniature barchans (Bagnold op.cit. pp. 208-109). Between these and the dune front the beach can be totally eroded (van Dieren 1934 p. 206, Schou op.cit. pp. 149-152). Inside the high water level line embryo dunes can be connected to the foredunes, organogenous, built up by tall grasses. Later higher dunes are developed. Inside the growing dunes there are often depressions, in Jutland also dune lakes.

Mobile sand can be transported from the rather hard windward side to the loose lee side. Though the dune individuals can move, the shape can be preserved, especially in the prolongation of wind furrows. Sometimes at strong erosion, the combined effect of deflation and corrosion, old dune bodies occur, as at Tönnersa, and the contrast between young dunes with accumulated sand and older eroded ones is very sharp. Parallel to the sand accumulation on lee sides, the deflation area advances and a pattern for a migrating dune occurs, a parabola dune with the opening windwards. In the south part of Tönnersa such dunes have increased in the last years, as the outer dune front has been broken on several parts. At Sandhammaren and Furuboda parallel to the coast line dune rows are present. Further inland they are broken and transformed to parabola dunes. If such dunes begin to move, the normal form is a barchan. Migrating dunes are not found in South Sweden on the mainland but occur for instance on the island of Gotska Sandön (Selander 1957 p. 144).

Linné (1749) saw initials to the small island of Måkläppen, outside the peninsula of Falsterbo. About 1770 *Elymus arenarius* settled (Lidbeck, A. 1795). The island has changed in morphology and size during the two hundred years until today (Gertz 1948). The configuration after 1925 can be seen in Davidsson (1963 p. 164).

Ardö (1950, 1957) has studied coastal changes at Tönnersa and found that a dune area on a beach bar increased 800 m from 1840 to 1942, about 8 m/year. He has estimated that new sand tongues need 25-40 years to be stable enough for pioneer plants to colonize, often *Honkenya peploides*. After 50-75 years *Elymus arenarius* immigrates with seeds. The

beach bar, near the outlet of the river *Genevadsån*, debouches to the north today but not on the map of Brandberg (1819). In the dune areas near Ystad and Åhus the rivers also have changed direction in the 19th century. The estimated dune growth at Tönnersen is about 1 m/10 years. Investigations from the Bothnian Bay (Eisquist 1944) and from the south parts of the Baltic Sea (Kallmark 1911 p. 225) agree with the results of Ardt. It can be mentioned that the small forts from World War II in some places at Sandhammaren today are nearly buried in sand.

THE VEGETATION

The pines of the early postglacial survived in NE Scania and in the inner part of Halland but whether the recent pines could be original on the sands is very uncertain (see Hemberg 1904, cf. Petersens 1932). In South Scania *Quercus robur* dominated, in Halland *Q. petraea* was common, often together with *Q. robur* (Erdtman 1952 pp. 51-52). After the invasion of beech, the oak was remaining dominant on wetter or drier places, e.g., the sands. The earlier vegetation on and near sandy areas can be studied in pollen diagrams (Nilsson, T. 1935, Caldenius et al. 1966, Mohrén & Larsson, W. 1968).

According to Malmström (1939) the forests diminished in Halland during 1600-1800 as an effect of felling, grazing and burning. The burning and grazing destroyed the humus layer and in sandy areas the sand began to shift. In the 19th century the forests changed their character. Many sands were planted with pine. The Calluna heaths decreased (Nilsson, A. 1901, Schager 1909, Schotte 1921, Sjöbeck 1933, Malmström 1937, Romell 1952, Damman 1957, Malmer 1968 b) and are today covering only small parts of the landscape. In coastal Halland oak stumps, probably remnants from a burned forest, are present. In these forests oak could be mixed with pine, or in the Vomb plain and other inland sands with beeches (Bruzellius 1802 p. 5). A type of forest, now rare, was the acid wet forest composed of alders, birches and willows together with sedges, common both in the Vomb plain and along the coasts. Aggradation and winding rivers caused water-logged soils. However, as the sand continued to shift the peat was covered, a process rather similar to the conditions in the depressions just inside the dunes.

The landscape, especially in Halland, can be

divided into three zones, the coastal one with pines together with fields of arable land, the middle zone with beechwoods and the third bordering on the province of Småland with pines and spruces. Is it possible for the pine to survive in southwestern and southernmost Sweden and develop favourably there? Is the zonal differentiation original or of cultural influence? As in Denmark the rare occurrence of pine in the coastal zone during the 18th and 19th centuries could be an effect of negative cultural influence (Sernander 1902 p. 464, Hemberg op.cit. pp. 180-181). Probably the pine could have been more common before the 19th century. But many authors (Fischerström 1761 p. 238, Dahlbom 1777/78, Osbeck 1778 pp. 27-28, 1796 p. 39, Fries 1817-19 p. 145) have noticed only scattered pines in the coastal districts. Montin (1768 p. 269) was of the opinion that the pine is typical of the sands, Osbeck (1776 p. 64, 1796 p. 38) of soils occupied by heather.

The studied localities within the investigation area belong to the southern deciduous forest region or Nemoral zone (Sjörs 1963 pp. 110-111, 1965 pp. 49-52, 1967 pp. 104-108, 1971 p. 225). The inland sands in the province of Småland and the maritime sands at Böda on the northernmost part of the island of Öland are instead parts of the southern coniferous region or Boreo-nemoral zone (Sjörs op.cit.). The investigated vegetation, particularly the forest communities, is more connected to the Central European vegetation (see Passarge 1968) than to that of northern Scandinavia (see Kielland-Lund 1971).

A main part of the southern deciduous forest region consists of a poor oak forest on silicate soils (Weimarck 1947 c, 1950 pp. 137-139, Tüxen 1951 pp. 157-159). Richer deciduous forests occupy only small parts. A special element in the landscape is the area of calcareous soils with a continental climate in the eastern and south-eastern parts of Scania (Topografiska . . . Kristianstads län 1876 pp. 48-49, Sterner 1922, 1925, Andersson, O. & Waldheim 1946). In the oligotrophic area of western Sweden (Hård av Segerstad 1924, 1925, Granlund 1925), the Atlantic influence can be seen in the mires (Malmer 1965) and in the different dwarf shrub heaths (Malmer et al. 1965).

HUMAN INFLUENCE

Man has inhabited the sands since the mesolithic period. Near Ystad a people lived on the sands

before the surrounded mires were developed, about 6-7000 years ago (Jönsson 1934). More intense human influence dates from the Neolithic age. In general the sand started to shift probably later than 2-300 B.C. (see Caldenius et al. 1966 pp. 84-85). The forests were destroyed from early historic time on, and sands appeared and increased especially during the Middle Ages, probably followed by a decrease when the forests again covered larger areas.

From the beginning of the 16th century different documents report on sand shifting. The origin of Lynga dune near Haverdal has been determined to about the year 1500. A small village, Åmot, near the outlet of the river Lagan, had in 1550 five farms, 100 years later only one. The abandonment of the village of Haverdal occurred in the 16th century. Danish actions to stop the sand shifting are registered from the 16th and 17th centuries, particularly in the fields at Ängelholm and Falsterbo, Swedish in the 18th and 19th centuries. At Ängelholm and Åhus the sand shifting was severe. At Åhus the dune vegetation was destroyed at the time of the siege of Kristianstad in 1677-79 or just afterwards (Bergstedt 1931). The sands at Sandhammaren and Vomb shifted later.

In the 18th century the sand shifting reached its maximum and caused the people serious problems. Near Sandhammaren a fishing village had to be moved, in 1742, to the north side of the esker Kåsebergaåsen (Moberg 1895). Another fishing village, near the town of Ystad, was totally missing on a map from 1767 (Jönsson op.cit.). At Falsterbo, according to Lidbeck, E.G. (1759), strong plants were changed into mountains of sand.

In 1795 the sand was as well covered with heather as uncovered. Lidbeck, E.G. (op.cit.) says the most severe damage along the coast appears in March-April, before the plants have started to grow.

The first Swedish actions to stop the sand shifting on the dune fields at Falsterbo started in 1720 and at Ängelholm in 1739 (see Montin 1768). A wide area had been devastated since about 1680 (Glimberg 1955 p. 126). At Sandhammaren Cronberg (1762) reported large dunes. There the mobile sand occurred during the 19th century and did not cease until the beginning of the 20th century, much later than other sands in South Sweden.

From the middle of the 17th century the western parts of Halland consisted of arable land, meadows, mires, heaths and sands near the coast. The sand shifting destroyed many of the coastal meadows. Ac-

cording to Malmström (1939) the grazing and heather-burning contributed to the decreasing of the forests, keeping the area in a forest-free state from 1650 to the end of 1800. The nuisance of the blown sand can be seen in a large dune near the church of Snöstorp. Osbeck (1796 p. 41) says that the cutting of turf, forbidden in Scania since 1779, changed the heaths into sands, more than the decrease in forest area. To get better heather the heaths were burnt in spring. On several heaths there had grown pines, as remaining stumps and roots show, but also seedlings and juvenile pines and birches were common. In some places the people regarded the oaks in the fields as impediments (see Osbeck 1776 p. 63, Barchaeus 1773 p. 97) and certain conditions to remove the oaks were given. Though the oak forests probably earlier occupied large areas, as find of oak stumps indicate (Mellström 1914), the decrease in number of oaks was so severe that a Royal Ordinance protecting the oak forests in the country was issued in 1746. On the coastal sands at Åhus and Sandhammaren the oak forests had been destroyed probably in the middle of the 17th century. Thus the Admiralty Staff tried to start a general inventory of the oaks. In 1749 a Charter concerning oak and pine cultures was proclaimed (Malmström op.cit. p. 214).

Near the coast the heather and also the dune grasses were utilized for fuel which contributed to increasing the sand shifting, sometimes parallel to actions with small shrubby fences to stop the blown sand. The border between arable land and the dunes was often diffuse. Aspects of the burning of coastal forests are to be found in Cronberg (1762), Mellström (op.cit.), Richter (1929), Malmström (op.cit.), Löfström (1946) and Olsson, H. (1972 a).

In the village of Hemmestorp in the Vomb plain the problems with the sand were trivial in 1705, but between 1774 and 1817 the sand shifting increased (Glimberg 1964) as a result of cultivation of the sandy soils. A similar development occurred on the large Kristianstad plain. From other parts of the Vomb plain damages have been reported by Lidbeck, E.G. (op.cit.) and Campbell (1928). The sands at Slättö Sand, in the province of Småland, probably shifted still later (Odencrants 1817, Wibeck 1906, Palm 1919). According to maps sand shifting reached a maximum there in 1817 and was only of small importance after 1871.

Linné (1749 pp. 336-341) and Lidbeck, E.G. (1759 p. 135) say that the Dutch several years ago planted dune grasses with their rhizomes; in Sweden also ears were sown. The plantations were most convenient in the autumn or early spring.

Cronberg (op.cit.) describes how tang can be put on the sand and thus preserve the wetness. Montin (op.cit.) says that nature does not well endure naked and uncovered soil. Concerning the plantations at Ängelholm Linné (op.cit.) relates that it is necessary to know the climate important for the plants. The result of the plantations seemed to be good (Linné op.cit. p. 340, Lidbeck, E.G. op.cit. p. 138, Retzius 1776 p. 15). Retzius (loc.cit.) noticed a shrubby wood with luxuriant oak, beech, birch, pine, ash, elm, aspen, and alder and proposed a plantation of the poor inland sands with different trees. Especially the planted aspen thrived and probably a statement in Warming (1909 p. 362) is wrong that aspen never has been planted in Sweden. Lindbohm (1891 p. 162) reports that the dunes at Ängelholm were covered with grasses in 1790.

Lidbeck, A. (1795) says that if the wet-growing heath on Skanör's Ljung near Falsterbo could be planted with a forest, it would be of great importance for this forest-free part of Scania. A severe problem was the cutting of turf. A Royal Charter from 1790 proclaimed planting of pine, but not until 1845 were the first stands of trees grown (Glimberg 1955 p. 130). Linné (op.cit.) describes small forests from Espet near Åhus and on sands near Ystad inside the outer dunes, and suggests that the SE Scanian pastures should be planted with pines to stop the sand shifting. The first plantations at Sandhammaren occurred in 1760, partly destroyed in 1770 (see Olsson, H. 1972 a). In the Vomb plain besides pine also *Elymus arenarius* was planted (af Petersens 1932 p. 26).

In the late 18th century the sands were large and the devastation of the forests also culminated as a result of heather burning and cultivation. In spite of efforts with shrubby fences the problems with the sand shifting accelerated. Charters from the Government concerning in 1790 and 1819 the Scanian sands and in 1821 the sands of coastal Halland were issued with orders to stop the blowing sand. Brandberg (1819) made an inventory of all coastal dunes of Halland. He mapped where the people suffered from the sand. The detailed description contains information about the height of the dunes, the

different plants and the qualities of the soils. In 1824 under the leadership of J.O. Bruhn, an expert from Denmark, a methodical plantation started. Pine cones, alder and birch seedlings, willow cuttings and rhizomes from different dune grasses were utilized. The results are presented in a report (Bruhn 1862).

Bruzelius (1802 p. 10) refers to a *Salix fusca* (probably *Salix arenaria*) as suitable to stop the sand shifting. He says that the yield of oak plantations is low and inferior to both birch and pine. Extensive pine plantations at Sandhammaren started in 1826 and the pine culture has continued until today. The sands in Kristianstad county (län) were surveyed in 1820 and C.S. Hofflander led the plantations from 1823 to 1836 (see Christianstads Läns Kongl. Hushålls-Sällskaps Handl. 1824-36). The first large stands with pine are reported from Åhus in 1837, probably a result of the actions in 1813 (Glimberg op.cit. p. 133), when the sands were resurveyed. In 1877 about 160,000 *Pinus sylvestris* were sown at Furuboda. As a rule there was a good growth of older seedlings. But the dry summer in 1878 and damage from roe deer caused that not more than 50 % of the plants survived.

Juvenile pines of three years' age were planted on the dunes at Tönnersa, pines of two years' age at Lynga (Haverdal) in 1876-79. On the latter sands 80 % survived at the end of the year. Too high precipitation could be harmful for the plantations in Halland. According to Lindbohm (op.cit.) some of the planted or sown pines at Ängelholm had given seedlings covering parts of the area. The first felling occurred in 1825. After 1870 *Pinus mugo* was planted on a large scale. Especially at Tönnersa also the cultivation with dune grasses continued. Of interest were the experiments to plant both *Alnus incana* and *A. glutinosa* (Noreen 1891). At Sandhammaren pine cones, birch seedling and acorns were used (Warming op.cit. p. 263). The pine cones were from different parts of Sweden and from other countries (Hemberg 1904).

The many forest plantations led to a decrease of the sands. Also the arable land enlarged and sandy relicts were cultivated. But too hard grazing or wrong cultivation caused new erosion problems, which can be seen in places in the Vomb plain (Rasmusson 1962). In spite of smaller areas the sands are still an important component in the South Swedish landscape. On the other hand, new sites have been colonized and specific habitats are

developed on verges, sand pits and military training camps.

In the late 19th century the sands, covered with pines, on several places have been drained, at Tönnersa in 1876-79 and this has been continued until today. At Tönnersa also efforts to replace the pine with the spruce could be seen in a few stands. Near the small river Tygeån at Sandhammaren a cultivation project was undertaken about 1890 and in 1909-13 great parts of the mire Hagestads mosse were drained. Today parts of the sands are nature

reserves and they have importance as recreation areas. But increased human activity leads to different erosion problems particularly along the coasts (see Norrman 1971). Also animals can influence the sands, e.g., the burrowing of the rabbits. The grazing by moose and roe deer has importance for the vegetational succession.

Grazing by domestic animals has influenced the coastal sand vegetation strongly, but is now decreasing, which has resulted in conspicuous changes (Pettersson 1965).

The flora

The number of species within the investigation area have been rather constant during the last centuries. Of disappeared or nearly absent species can be mentioned *Filago apiculata* and *F. germanica* (see Nilsson, Ö. 1968). Different species such as *Dianthus arenarius* and *Androsace septentrionalis* have lost certain outposts in the inland, *Asparagus officinalis* and *Lepidium latifolium* probably along the coasts. In general most species are common even today though the sands have decreased.

The flora lists given by Cronberg (1762) and Montin (1768) may be compared with the number of plants found today. To judge from Montin (op.cit.) *Corylus avellana*, *Genista pilosa*, *Antennaria dioica*, and *Polygonatum verticillatum* seemed to be more common earlier in coastal Halland. Also the reported *Lichen nivalis*, probably *Cetraria nivalis*, is very uncommon today (Hasselrot 1953). At Sandhammaren *Arctostaphylos uva-ursi*, *Antennaria dioica*, and *Cladonia dactylota* seemed to be more common earlier in the open heath landscape. *Juniperus communis*, earlier common on the maritime sands in Halland, is now reduced in abundance. It is at present nearly absent at Sandhammaren. Cronberg (op.cit.) mentioned *Cladium mariscus*, *Ledum palustre*, and *Oxycoccus palustris*, today all disappeared from Sandhammaren. The number of *Vaccinium vitis-idaea*, *Myrica gale*, and probably also *Vaccinium myrtillus* have been strongly reduced on the same sands. From other places also in South Sweden von Post (1863) noticed the decrease of different dwarf shrubs. Montin (op.cit.) reported scattered *Pinus sylvestris* on the coastal dunes in Halland, but there are no registrations on the map drawn by Malmström (1939). Both Cronberg and Montin have noticed *Populus tremula* as rather common along the coast. The oaks are called only 'Quercus' at Sandhammaren or 'Quercus robur' (including *Q. petraea*) on the dunes in Halland. Cronberg reported two species of alder, *Alnus incana* and *A. viscida*; today only the later (*A. glutinosa*) is found at Sandhammaren. Parts of the

maritime dunes in Halland have been planted both with *Alnus glutinosa* and *A. incana* (Noreen 1891 p. 165) but the latter is not found today and is probably extinct.

According to Selander (1957) and Pettersson (1958, 1965) certain species, such as *Lathyrus maritimus*, *Petasites spurius* and the maritime type of *Solanum dulcamara*, have increased their area of distribution. *Ammophila x baltica* seems to have increased its range both on the west and east coasts in recent time, in Areschoug (1881 pp. 535-536) only on the east coast. As a consequence of the weak competition new species immigrate on the sands. *Senecio vernalis* was introduced into Sweden about 1860. It is now very common in the inland, but also spread along the coasts (Hultén 1971). *Holcus mollis* is in places in the Vomb plain found together with *Senecio vernalis* and *Erigeron canadense*. *Atriplex sabulosa* has colonized new areas along the west coast, due to a small difference in the climate during the last 30 years. *Rosa rugosa* planted on the dunes to stop the sand shifting is now naturalized (Weimarck 1963).

Many plants growing on the maritime sands have developed specific morphological forms, ecotypes (Turesson 1922, 1925). Often these coastal taxa differ from corresponding plants in the inland (Jalas 1950, Lökvist 1962) as *Hieracium umbellatum*, *Jasione montana*, *Viola canina*, and *V. tricolor*. Of special interest are low-growing forms of *Galium verum*, *Lotus corniculatus* and *Anthyllis vulneraria*. Often hairy variants can be developed as *Armeria maritima* var. *elongata* (see Turesson 1922 p. 274, Hylander 1955) and *Solanum dulcamara* var. *marinum* (see Neuman & Ahlfvengren 1901, Turesson op.cit. p. 230), the first one also on inland sands. *Festuca arenaria*, *Salix arenaria*, and *Tripleurospermum maritimum* are regarded as species.

The South Swedish flora can be divided into several phyto-geographical groups (Areschoug 1866, Sterner 1922, 1925, Hård av Segerstad 1924, 1925,

Weimarck 1950, Olsson 1972 a). The oceanic element (Degelius 1935) has few eu-oceanic representatives within the investigation area, as *Erica tetralix*, *Bromus hordeaceus* ssp. *Thomini* and *Lonicera periclymenum*. They can also be regarded as sub-oceanic species. A second group is the suboceanic element: *Aira praecox*, *Filago minima*, *Corynephorus canescens*, *Galium saxatile*, *Hydrocotyle vulgaris*, *Juncus squarrosus*, *Ornithopus perpusillus*, *Teesdalia nudicaulis*, *Cladonia dstricta* (see Barkman & Westhoff 1969), and *C. strepsilis* (see Degelius op.cit. p. 3). Several species, such as *Alnus glutinosa*, *Betula verrucosa*, *Geranium sanguineum*, *Lathyrus montanus*, and *Myrica gale*, belong to the southern element. The southeastern or south continental element, with many subcontinental plants, is represented by *Anthericum liliago*, *Artemisia campestris*, *Cynanchum vincetoxicum*, *Festuca polesica*, *Helichrysum arenarium*, *Koeleria glauca*, *Peucedanum oreoselinum*, *Phleum phleoides*, *Viola rupestris*, and *Cladonia mitis*. In South Sweden *Dianthus arenarius*, *Astragalus arenarius*, and *Anemone pratensis* are steppe plants, further to the east rather common in thin pine forests. *Ledum palustre* belongs to a northeastern element (see Areschoug op.cit.). The northern element includes *Elymus arenarius*, *Lathyrus maritimus*, *Linnaea borealis* and *Juncus balticus*.

In the flora list below only a small part of the different taxa, found within the investigation area, is treated, with special remarks on distribution, morphology and ecology.

Quercus

Q. petraea only at Haverdal, possibly including *Q. petraea* x *Q. robur*. Montin (1768) has noticed *Q. robur* on the dunes; probably also including *Q. petraea*. Today *Q. robur* seems to appear on a few marginal dunes somewhat inland at Tönnersa. Fries (1817-19) included in *Q. robur* both a form *pedunculata* and also *Q. sessiliflora* (= *Q. petraea*). Weimarck (1947 a, b, c) has studied the oaks in South Sweden, where the distribution of *Q. petraea* coincides with *Q. robur* x *Q. petraea*. At Sandhammaren *Q. robur* ssp. *puberula* is present (Weimarck 1947 a). *Q. petraea* could be rather high-growing. The leaves have long stalks and the cupules are lacking stalks. The oak regeneration under the canopy of pines on poor soils is in some places very good.

Rosa

R. rugosa, an Asiatic plant (see Ohba et al. 1973), has been planted on the dunes in South Sweden and Denmark, become naturalized and spread on many places this cen-

tury (Østergaard 1953/54, Jessen 1958, Weimarck op.cit.). *R. rugosa* is supposed to be spread by the sea. The germinating ability is nearly unchanged after having floated six weeks (Jessen op.cit.).

Salix

S. aurita has leaves with more distinct nerves than *S. cinerea*, which is more common on eutrophic habitats (see Weimarck 1963). —*S. caprea* is found in some places as at Furuboda in the shrubby vegetation on back dunes. —*S. pentandra* forms small stands just behind the outer dunes on wet places at Tönnersa. —*S. arenaria* is typical and frequent in *Salicetum arenariae*, occurs in *Salici-Empetretum* on maritime sands and is scattered in the Vomb plain. *S. arenaria* forms cycles on the sand and needs a wet milieu to germinate (Ranwell 1960 p. 133). The related *S. repens*, common in wet meadows and mires, seems to lack this quality. The shrub of *S. arenaria* varies from creeping to high-growing.

Armeria

A. maritima var. *elongata* (see Neuman & Ahlfgvengren op.cit., Hylander 1955) with hairy leaves is common on dry sand, especially seen at Falsterbo together with *Aira praecox*. The inland plants of *A. maritima* could resemble this var. *elongata* but also differ (Turesson op.cit. p. 272). Krausch (1968 a) has proposed an alliance *Armerion elongatae*.

Anthyllis

A. vulneraria consists of many forms (Jalas op.cit.). In inland sands, sandy hills or abandoned sand pits, *A. vulneraria* is high-growing with pale yellow flowers; on maritime sands grow plagiotropic plants with red flowers (see Hallberg 1971). The species can winter with a rosette.

Artemisia

A. campestris varies considerably in the field. When growing on blown sand it is distinguished by greyish-white hairiness and a more upright habit of growth (Turesson 1925 p. 149), treated as a subspecies by Neuman & Ahlfgvengren (op.cit.), and regarded a specific dune ecotype. *A. campestris* is common on dry sandy fields, not too poor soils, in South Sweden. According to Hultén (1971) *A. campestris* is more frequent in North Jutland and Sealand and in the East Baltic area. Fukarek (1961) has proposed a *Helichryso-Artemisietum balticum*, an East Baltic vicariant to *Violo-Corynephorretum*. —*A. vulgaris* could be found in perennial drift vegetation.

Asparagus

A. officinalis is probably native along the South Swedish coast (Hultén op.cit.) and anthropogenous at Ålstorp in W Scania.

Atriplex

A. calotheca, found only on annual drift vegetation at Falsterbo, has large triangular lacinated bracts. —*A. glabriuscula* co-exists with other species of the genus, e.g., *A. latifolium*, and hybrids are common, on the western

coast more frequent than *A. glabriuscula* itself (Turesson 1922 p. 246).—*A. latifolium* has been separated into two forms, one hereditary prostrate form and a second erect form (Turesson 1919 p. 27).—*A. littoralis* grows in a more erect form in the Sound region compared with the northern west coast parts with plants of lower stature (Turesson 1922 p. 245), seen at Tönnersa and Haverdal.—*A. sabulosa* with a creeping prostrate growth is very scattered in *Cakiletum maritimae*, or sometimes solitary in front of *Elymo-Ammophiletum* from Haverdal to Ängelholm.

Cerastium

C. semidecandrum coll. is common on the calcareous sand at Vitemölla, where small forms of *C. glutinosum* could be included. In the rare *Tortulo - Phleetum arenarii* at Falsterbo *C. semidecandrum* coll. could consist of *C. glutinosum*, *C. subtetrandrum*, and possibly also *C. atrovirens*, an eu-oceanic element and a dune plant in Jutland (Iversen 1936 p. 100).

Dianthus

D. deltoides is found rather scattered in the sandy grassland or dry meadows. Like *Artemisia campestris*, *D. deltoides* is less common in Scania compared with East Denmark, middle parts of Sweden, and the Baltic States.—*D. arenarius*, with several geographical races (see Jalas op.cit. p. 17), forms small low growing mats, rosettes, on the surface. *D. arenarius* found on several places in East Scania is noticed from sandy hills in southern Halland by Theorin (1865).—*D. superbus* seems to have increased at Sandhammaren during the last years. Hallenborg, T. (1956) has reported the species from the northernmost place in Sweden, near the outlet of the river Genevadsån in the province of Halland. Montin (1766) says that *D. superbus* grows in abundance near Halmstad.

Dryopteris

D. austriaca is rather common at Sandhammaren, in dune depressions or of a *Pseudopinetum* on Järarna, the beach ridges behind the dune landscape.—*D. spinulosa* is common in different dune depressions within the investigation area, or in juvenile forms on the dunes.—*D. filix-mas* is less common or scattered.

Erodium

E. cicutarium is typical of culture soils. In the sandy grassland several types could appear as *E. cicutarium* ssp. *dunense* on maritime sands (Larsen 1958) and probably on the calcareous slope at Vitemölla. A plant with a strongly, flattened, prostrate growth on the sandy golf links at Falsterbo is different and seems to belong to the complex of *E. glutinosum*, which is a characteristic taxon of *Tortulo - Phleetum arenarii* (Westhoff & Den Held 1969).

Eryngium

E. maritimum has in the Baltic area a northern outpost on the island of Gotska Sandön. The species is a

characteristic taxon of *Ammophilon borealis* but can also grow in a contact vegetation in rather closed stands of *Carex arenaria* and *Tortula ruralis* var. *ruraliformis* (Friesendahl 1926, Paul 1953, Pettersson 1958 p. 151). The vegetative regeneration has only small importance for the plant distribution. The scattered individuals in Sweden seems to be a result of dissemination (Friesendahl op.cit.).

Galium

G. verum is common on the sandy dry grassland as well as rather nitrophilic places, preferring light and warmth, not dependent on a calcareous soil (Hallberg op.cit.). *G. verum* var. *littorale*, reported from the province of Bohuslän by Hallberg (op.cit.), seems to be missing in South Swedish maritime sands and is substituted by a complex of taxa of low rank (Lövkvist op.cit.).—*G. saxatile*, a suboceanic element, has been found in *Pseudopinetum* at Sandhammaren and in the Vomb plain corresponding to a *Galio- Pseudopinetum sylvestris* (Passarge 1962).—*G. aparine*, possibly var. *marinum*, could exist in the drift vegetation (see Hylander op.cit.) from Haverdal to Falsterbo.—*G. palustre* is more common in *Irido - Alnetum glutinosae* than *G. uliginosum*, rather frequent in the periodically inundated *Molinio - Myricetum gale Salix arenaria* subass.

Hieracium

H. pilosella includes a lot of clones and biotypes separated through leaf form and hairiness (see Weimarck 1963 p. 670).—*H. umbellatum* is divided into several ecotypes also varying along the coasts (Turesson 1922, Lövkvist op.cit.). In this work the plant is named *H. umbellatum* on inland sands and *H. umbellatum* ssp. on maritime sands.

Jasione

J. montana is frequent on the inland sandy grassland. On coastal dunes a typical *J. montana* var. *littoralis* is developed.

Lotus

L. corniculatus has been studied by Jalas (op.cit.). He has distinguished a maritime form with a western distribution, found in *Salici-Empetretum* from Haverdal to Falsterbo.—*L. tenuis* is found at Sandhammaren in a salt/fresh gradient community belonging to *Loto-Trifolion* (Westhoff & Den Held op.cit. p. 107).

Linnaea

L. borealis has increased its area of distribution through the afforestation along coastal sands both in South Sweden and in Denmark (see Hultén op.cit.). According to Neuman (1884 p. 12) *L. borealis* immigrated 30-40 years after a pine plantation had been performed at Tönnersa.

Solanum

S. dulcamara is a characteristic taxon of *Irido - Alnetum glutinosae* and there represented by an inland type according to Turesson (op.cit.). He has also noticed a succulent

type along the west coast seashores, probably identical with *S. dulcamara* var. *marinum* found in the drift vegetation at Ängelholm and Falsterbo.

Viola

V. canina is split into ssp. *canina* and ssp. *montana* (see Weimarck op.cit.). Studied plants belong probably to the first subspecies. In this work the inland forms are regarded as high rank taxa. On the maritime sands *V. canina* ssp. *canina* var. *dunensis* following Garke (1972 p. 948) in the text and tables is written *V. canina* var. *dunensis*. This taxon with elongated leaves and showing plagiotrophy, is characteristic of *Violo-Corynephorum* on maritime sands and seems to correspond to a var. *sabulosa*, an ecotype proposed by Clausen (1931). Both *V. canina* and *V. tricolor* appear as perennials, more rarely annuals, on the coastal dunes, rather different from the inland types.—*V. tricolor* ssp. *curtisii* (see Garke op.cit. p. 954) has large flowers, a vertical stock and is not or scarcely creeping on the sand. This taxon is found on dunes and dry grassland near the sea in W Europe and in the Baltic region, and corresponds to a ssp. *maritima* on Jutland dunes (Clausen op.cit.).—*V. rupestris* is found in Antherico - Koelerietum *glaucae* at Vitemölla.—*V. riviniana* is scattered in *Agrostio - Quercetum roboris* in the Vomb plain.—*V. palustris* appears in moist or wet places on the west coast.

Agropyron

A. junceum ssp. *boreoatlanticum* occurs on seashores in W Europe and the Baltic region and is a characteristic taxon of the North-Atlantic *Elymo - Agropyretum junceiformis*.—*A. x acutum* is a hybrid between *A. junceum* ssp. *boreoatlanticum* and *A. repens* (see Hansen 1959-60). This taxon is more luxuriant than the previous one and is typical of perennial drift vegetation, characteristic of *Honkenyo - Agropyretum acuti*. The distribution partly coincides with *A. junceum* ssp. *boreoatlanticum* in South Sweden.—*A. repens* belongs to *Agropyro - Rumicion crisp* and is often found together with *A. x acutum* but on more nitrophilic places.—*A. pungens*, not found within the investigation area, occurs on the Jutland dunes. Both *A. pungens* and *A. x acutum* are characteristic taxa associated with *Agropyrete* *pungentis* (Géhu & Géhu 1969).

Agrostis

A. tenuis is very common in the dry sandy grassland, along the coast on degenerated dunes in the *Pleurozium schreberi - Agrostis tenuis* comm. at Ängelholm as well as in the shrubby *Agrostis tenuis - Populus tremula* comm.—*A. canina* is split into ssp. *montana*, frequent and a characteristic taxon of *Teesdalia-Corynephorum* in the inland but rare or missing on maritime sands. *A. canina* ssp. *canina* (Weimarck op.cit.), in this work treated as a high rank taxon, grows in some places in the dune depressions.—*A. stolonifera* has been seen in the border zone between lower parts of the back dunes and the edges of the dune depressions at Tönnersa and Ängelholm.

Montin (op.cit.) has noticed *A. stolonifera* on the dunes at Haverdal.

Ammophila

A. arenaria is a characteristic taxon of *Ammophilion borealis*, specialized with rapidly growing underground organs as well as curled leaves.—*A. x baltica* is a hybrid between *A. arenaria* and *Calamagrostis epigeios*. Vestergaard (1941) has pointed out three varieties. The vegetative regeneration seems to be predominant. Compared with *A. arenaria* the leaves are greener and more flattened. Compared with *Calamagrostis epigeios* the leaves are less hairy and more supple. The latter taxon can form clones on dry sand, close to separated clones of *A. arenaria* or of *A. x baltica*. At Sandhammaren *Calamagrostis epigeios* grows in wet or moist sandy habitats.

Carex

C. arenaria has a horizontally growing rhizome with shoots perpendicular in all directions (Erikson 1896 p. 27).

Corynephorus

C. canescens is a pioneer species, partly evergreen as *Ammophila arenaria*, potentially long-lived perennial, as long as sand accretion is taking place, growing most vigorously where there is up to 10 cm of sand accretion per year (Marshall 1967). The plant is vertically growing without rhizome. The roots are mainly directed downwards. Rychnovská-Soudková (1961) has shown the low dry resistance of *C. canescens* in the eastern limit of its distribution.

Elymus

E. arenarius is a seashore plant, also anthropochorously spread in the inland (see Hård av Segerstad 1924 p. 57). The nitrophilic plant belongs to *Honkenyo-Elymetea* (Tüxen 1970) and the vicariant class *Agropyrete* *pungentis* (Géhu & Géhu op.cit.).

Festuca

F. arenaria (Osbeck 1788, Kjellquist 1964) is more hairy and with longer runners than *F. rubra* and differs in habitats. The first taxon is common on maritime sands, the second scarcely on certain wracks and scattered in the inland sandy grassland.—*F. ovina* is common on the sands at Revingehed and Björka in the Vomb plain, as well as on dunes and beach ridges at Falsterbo.—*F. polesica* occurs in the Baltic region, from Falsterbo to Furuboda within the investigation area. *F. polesica* has more pointed leaves than *F. ovina*.—*F. trachyphylla*, common in East Scania, is probably a ruderal plant somewhere on the golf links at Falsterbo and on a few places at Sandhammaren.—*F. arundinacea* is rare in *Honkenyo - Agropyretum acuti* at Falsterbo.

Juncus

J. balticus occurs scattered along the coast both in rather

moist deflations poor in vegetation but often with *J. bufonius* and *J. filiformis* as at Tönnersa. Warming (1909 p. 332) has shown even more *Juncus* spp. and also hybrids in such deflations. Another habitat is a community corresponding to *Empetro-Ericetum* (Westhoff & Den Held 1969 p. 216) with scattered *J. balticus* at Ängelholm and just south of Halmstad.

Koeleria

K. glauca has a very short horizontally growing rhizome, without stolons (Erikson op.cit.).

Phleum

P. arenarium grows in the fragmentary *Tortulo - Phleetum arenarii* at Falsterbo. The plant seems to be bound to calcareous soils as at Vitemölla and the shell banks in the province of Bohuslän (see Hallberg op.cit.).—*P. phleoides* is found on grassy hills together with *Geranium sanguineum* in the marginal parts of the dune landscape at Sandhammaren.

Phragmites

P. communis is an eutrophic plant in the dune depressions, also rarely climbing on the dunes.

Brachythecium

B. albicans is not common on the investigated sands, more frequent in pastures. The species is rapidly prominent amongst the true pioneer mosses as *Ceratodon purpureus* and *Tortula ruralis* var. *ruraliformis* (see Birse et al. 1957).—*B. rutabulum* has a broad amplitude from dry dwarf shrub heaths and forests to stands with a rather moist milieu.—*B. reflexum* occurs in *Filipendulo - Alnetum glutinosae*, *B. velutinum* in not too dry oak forests.

Ceratodon

C. purpureus is, together with *Polytrichum piliferum*, the most common pioneer moss on South Swedish sands. The species has a good ability to withstand burial by sand. The maximum depth through which emergence took place is about 4 cm (Birse et al. op.cit.).

Dicranum

D. scoparium is typical on fixed dunes, heaths and forests. Re-establishment is slow and incomplete after burial by sand and not more than 2.5 cm can emerge thin leafy shoots on the ground (Birse et al. op.cit.).—*D. undulatum* is mainly found in the pine forests.

Drepanocladus

D. fluitans is seen in wet dune depressions at Sandhammaren, located in poor/rich gradient habitats.—*D. exanulatus* occurs in the periodically inundated western dune depressions, sometimes difficult to distinguish from *D. uncinatus* scattered in moist milieus.

Hypnum

H. ericetorum grows in dwarf shrub heaths, often frequent

in South Sweden (Nyholm 1954-69 p. 589).—*H. cupressiforme* is a strongly variable taxon, in this work named *H. cupressiforme* coll. as a rule. At Vitemölla and Falsterbo *H. cupressiforme* var. *lacunosum* occurs, a robust brownish plant growing on rather calcareous soils. At Haverdal the effects of inundation in wet or moist habitats make it difficult to differentiate *H. cupressiforme*, *H. ericetorum* and possibly also *H. lindbergii* from each other (see Nyholm loc.cit.).

Pohlia

P. annotina is reported from Sandhammaren by Warming (1909 p. 362) in open or semi-open moist dune depressions, today also found in the moss mat covering the soil in the salt/fresh gradient habitats.—*P. nutans* is found on decaying wood in wet or dry milieus as well as on the soil in heaths. Scattered and undeveloped *P. nutans* is seen in degenerated *Elymo-Ammophiletum*, especially in dense mats of *Ceratodon purpureus*.

Polytrichum

P. piliferum is an effective sand binder with living rhizoids down to about 6 cm (Warming op.cit. p. 237, Birse et al. op.cit.).—*P. juniperinum* is less common on maritime sands, seems to prefer a rather moist soil with a humus mixture. The ability to emerge after sand burial is about the same as for *P. piliferum* but slower in re-establishment.—*P. commune* is common in different wet dune depressions, especially at Sandhammaren, where Warming (op.cit. pp. 362-363) has differentiated *P. commune* and *P. perigoniale*, according to Nyholm (op.cit. p. 681) only a variety of *P. commune* in somewhat drier habitats.—*P. formosum* occurs rarely.

Rhacomitrium

R. canescens appears on the edge of hollows in the margin of *Salici-Empetretum* at Tönnersa or in blowouts with *Cladonio-Corynephorretum*, as at Sandhammaren and Furuboda.

Scleropodium

S. purum is common both in coniferous and deciduous forests as well as scattered in the dry sandy grassland. The species is typical of *Galio-Pseudopinetum sylvestris* (Passarge op.cit., Hofmann 1964).

Sphagnum

S. recurvum, probably *S. apiculatum* following Malmer (1966), named *S. fallax* in Nyholm (op.cit.), is very characteristic of the dune depressions.—*S. fimbriatum*, *S. palustre*, and *S. squarrosum* are also common.

Tortula

T. ruralis var. *ruraliformis* grows in loose yellowish mats but is less common from Falsterbo to Furuboda. The taxon seems to prefer calcareous soils but is also found on strongly anthropogenous sites.

Cephaloziella

C. sp., probably *C. divaricata* (see Arnell 1956 p. 70), is very common in most places.

Lophocolea

L. heterophylla is common on shady soils in rather high-growing dwarf shrub heaths, especially on decaying wood. The name has been used in the classification of *Salici-Empetretum Lophocolea heterophylla* subass.—*L. bidentata* appears among mosses in pine afforestations. *L. bidentata* and *Rhytidiadelphus loreus* with a western distribution are differential taxa of *Polypodio-Empetretum* (Westhoff 1947), related to *Salici-Empetretum Polypodium vulgare* subass. in South Sweden, to the Baltic variant *Salici-Empetretum*.—*L. cuspidata* is rare in *Irido-Alnetum glutinosae*.

Cetraria

C. crispa, a taxon of uncertain rank, is common at Ängelholm, more rarely found in the inland.—*C. islandica* seems to occur on most sands.—*C. glauca* together with *Evernia prunastri*, *Usnea hirta*, *Parmelia physodes*, and probably also *P. furfuracea*, epiphytically in the inland, are found both epiphytically and in a few cases living just on the surface on maritime sands, according to Westhoff (1947 p. 87) a feature of eu-Atlantic regions.—*C. nivalis* is rare in the investigation area (Hasselrot 1953, Mattiasson 1971).

Cladonia

C. floerkeana, very common on exposed soils, can include *C. bacillaris* at Sandhammaren and Vitemölla, with fine soredia and thin pointed podetia.—*C. pleurota*, closely related to *C. coccifera*, is common in the open dry sandy grassland, but on less exposed stands compared with *C. floerkeana*. The podetia are soredious, often only with pycnids (see Olsson 1972 b). The taxon has importance as a pioneer together with *Polytrichum piliferum* and *Cornicularia aculeata* on the dunes.—*C. alcicornis* has a western distribution, common on open dry exposed stands. Albertson (1946 p. 220) has given a transitional form between *C. alcicornis* and *C. convoluta* with rhizoids and larger phylloclads. The plants at Vitemölla could be related to this form or possibly be a variety of *C. convoluta*.—*C. strepsilis* is distributed in SW Sweden (see Magnusson 1929, Degelius 1935) in some places on heaths, where the precipitation water has difficulties in infiltration, viz., sites with *Erica tetralix* and *Gymnocolea inflata* as at Haverdal.—*C. chlorophaea*, similar with *C. pyxidata*, can be divided into several chemotaxa (Ahti 1966 pp. 380-390). According to Ahti (op.cit.) *C. chlorophaea* characteristically has coarse but distinct soredia on the outer and inner surfaces of the cups possibly narrower than in *C. pyxidata*. The habitat is moderately acid.—*C. grayi* is an allied chemotaxon of *C. chlorophaea* on highly acid habitats found on heaths in coastal districts (see Klement 1956/57 p. 925), also on maritime sands in South Sweden. *C. grayi* favours open or slightly shaded habitats, *C. pyxidata* and *C. chlorophaea* most abundant in shade (Ahti op.cit. p. 383).—*C. pyxidata* is difficult to distinguish from *C. chlorophaea* on dry sandy soils, though *C. pyxidata* normally grows on mineral soils and may be prominent especially on inland sands, with a substrate range from oligotrophic to eutrophic. In

this work both complexes of *C. chlorophaea* and of *C. pyxidata* are combined and named *C. chlorophaea* coll.—*C. fimbriata* has soredia uniformly covering the cup and seems to prefer more humus-rich soils than *C. chlorophaea* coll.—*C. cornutoradiata* is very common at Sandhammaren on fixed dunes.—*C. gracilis* is similar to *C. cornuta*. In *Violo-Corynephoretum* and *Cladonio-Corynephoretum* the plants seem to be damaged by the heat and radiation in the open stands and thus difficult to distinguish. *C. gracilis* is regarded the more common. In dwarf shrub heaths both specimens exist but *C. gracilis* is more frequent. In the tables the two species are included.—*C. elongata* seems to occur very rarely at Björka in the Vomb plain.—*C. degenerans*, *C. verticillata* and *C. glauca* are frequent on inland sands and are regarded as differential taxa of *Teesdalia-Corynephoretum*. *C. glauca*, in habit resembling *C. cornutoradiata*, common on South Swedish sands (Du Rietz, G.E. 1952 p. 127) though mainly distributed in the sub-Atlantic region (Klement op.cit.).—*C. furcata* is common or frequent on both siliceous and calcareous soils.—*C. rangiformis* seems to be weakly basiphilic, also growing in pastures.—*C. dstricta* has isolated occurrences along the coasts, most striking in *Cladonio-Corynephoretum* at Sandhammaren and Furuboda, growing on more exposed soils than *C. uncialis*. *C. dstricta* with a western distribution, has bluish grey podetia more prostrate than *C. uncialis*.—*C. rangiferina*, characteristic taxon of *Cladonio - Pinetum sylvestris*, is less common than *C. arbuscula* and *C. impexa*. The related *C. tenuis* has not been observed or is included in other *Cladonia* spp., according to Ahti (1961 pp. 60-61) the species is common along South Swedish coasts varying in habitat from forests to dry dunes. Magnusson (1929) says that *C. tenuis* is common only in the province of Bohuslän, otherwise rare.—*C. arbuscula* and *C. mitis* are combined, the first one is a characteristic taxon of *Cladonio - Pinetum sylvestris*, the second seems to be more prominent in the heaths, according to Ahti (op.cit. p. 123) only scattered within the distribution area.—*C. alpestris* is rare at Furuboda, the now southernmost locality in Sweden.

Cornicularia

C. aculeata is distributed on different dry sandy soils.

Peltigera

P. canina is probably the most common species on shady sites, *P. rufescens* on sun exposed places (Gams 1967).—*P. malacea* is growing in rather moist poor acid heaths as at Haverdal.

Stereocaulon

S. condensatum grows on open sand in dune districts (see Du Rietz, G.E. op.cit., Poelt 1969) together with *Cladonia dstricta*, *Rhacomitrium canescens* and *Pycnothelia papillaria*; at Furuboda also together with a second *Stereocaulon* sp. not determined.

Fungi

Several Fungi, not treated in this work, occur on the sands (see Osbeck 1762, Andersson, O. 1950 b).

Methods, nomenclature, terminology and abbreviations

The present investigation deals with the differentiation of the vegetation on aeolian and glacial sands in South Sweden. The vegetation is normally growing on acid siliceous soil, only rarely on calcareous ground. Some species can be regarded as acidophytes, others as weakly distinguished neutrophytes. The floristic composition is dependent both on climate and on edaphic conditions. Maritime and continental influences are striking. The analyses of the vegetation follow as far as possible the floristic composition in the arrangement of a plant sociological system. Sometimes the physiognomy, the structural organization, must be considered. The analyzed material gives the floristic sociological variation within the vegetation units and is shown with indicator taxa. The dominants in the studied plant communities also give ecological information.

The classification of the vegetation agrees largely with the floristic plant-sociological system worked out by Braun-Blanquet (1921, 1964), Tüxen (1937, 1955, 1970 b), and Oberdorfer (1957, 1968). In the sense of Braun-Blanquet (1959) and Oberdorfer (1968) an association had to contain characteristic species. In certain cases, especially in the siliceous districts, true characteristic species could be difficult to find. Instead taxa of low rank, subspecies and varieties with smaller sociological and ecological amplitude are used to separate the vegetation units, often associations. In the work of Westhoff & Den Held (1969) taxa are used throughout instead of species. Also in South Sweden it is necessary to use taxa. Sometimes characteristic or differential taxa combinations are applied. A group of differential taxa can also separate plant communities (see Knapp 1971 p. 61), e.g., *Agrostio-Callunetum* or *Agrostio-Quercetum roboris*. The division into characteristic and differential taxa, as well as companions and occasional taxa, is valid for the conditions within the investigation area. Thus indicator taxa or indicator taxa groups are mainly provincial, some with greater, others with smaller distribution.

The plant community system proposed by Du Rietz, G.E. (1921, 1936, 1957, 1965) was originally based upon the structural organization, the physiognomy, but in the later works, the medium and higher units were based on composition by species. The lowest unit, the sociation (Du Rietz, G.E. 1936), in the sense of Scandinavian plant sociologists is characterized mainly by the specific dominance in different layers. In the present work the sociation is regarded as a subunit of the association. Géhu & Géhu (1969) and Westhoff & Den Held (op.cit.) have placed the sociation outside the association. The vegetation has been studied by methods proposed by Du Rietz, G.E. (1957), especially the small square frequency determination. Within the segments or stands (Du Rietz, G.E. op.cit., and 1965 p. 25) possibly random dispersion, homogeneousness and 'minimum number' are supposed to be valid. The pattern can be disturbed by several microcoenoses, e.g., bryophyte communities in alder carrs. Analyzed small squares, 6-12 samples in every segment, have always been 1 m² to be comparable to other analyzed stands. The small square frequency and the characteristic degree of cover are calculated according to Malmer (1962 pp. 48-49). Taxa outside analyzed squares but within the segments are indicated with +.

Westhoff (1967, 1968) has discussed the vegetation structure as a classification criterion in the Braun-Blanquet system and has made an attempt to place the vegetation in the Netherlands in structural units. Doing (1962, 1963 a) as well as Scamoni et al. (1965) and Passarge & Hoffmann (1968) have used plant sociological groups with physiognomical aspects to give an objective classification of the vegetation, especially tall scrub and forest. The present author has used *Irido - Alnetum glutinosae* and *Vaccinio - Pinetum sylvestris*, both examples of this concept of sociological groups in a structural sense. In the intermediate Nemoral zone, between South European associations rich in species and North

European, boreal zone associations poor in species (see Ellenberg 1954 p. 136) the structure of vegetation can be an important complement to the Braun-Blanquet floristical system. The problems regarding limits of vegetation units (Dierschke 1969) can also be mentioned in this context.

Described plant communities are named as expressively as possible. Indicator taxa must be current for every vegetation unit. According to Ellenberg (1956 p. 66) it is not quite necessary to find characteristic taxa in every analyzed segment, but in parts of the investigation area. An example is *Cladonio* (dstrictae) - *Corynephorum* regarded as a northern fragment of *Spergulo-Corynephorum*. Subassociations and varieties are named after a specific taxon, rather common in the area of distribution. A subassociation, in certain cases, without differential taxa is called a typical subassociation. Floristical units are arranged in tables (Ellenberg op.cit., Braun-Blanquet 1964, Knapp op.cit.). The purpose is to present the composition of the vegetation in a phytosociological scheme, also of ecological importance. The characteristic taxa are placed before the differential ones. Companion taxa and occasional taxa are placed below all indicator taxa. The plant sociological system worked out has a regional limitation (see Knapp op.cit.) concerning the distribution of characteristic species. To the north there may occur outposts of the range. The geographical variation of the plant sociology is illustrated with vicariants. Thus the alliance *Ammophilion borealis* may be divided into four vicariant associations, viz., *Petasito-Ammophiletum*, *Elymo-Ammophiletum*, *Lathyro-Ammophiletum* and *Euphorbio-Ammophiletum* (Géhu, comm. at a Colloque in Paris 1971).

The soils have been investigated mainly according to Kubiëna (1953), Mückenhausen (1962), and Duchafour (1970). Registered soil types are syrosem, ranker, pararendzina, podsol, podsoloid, pseudogley, aue soil, anmoor fen soil, and fen peat soil. The stratification of soil (see Reuter 1956/57, Schroeder 1972), including the thickness of different horizons especially the humus layers, is important for understanding the composition of plant communities as well as vegetational changes. Soil texture, colour and root distribution in the course of eluvial and illuvial processes in the evolution of soils parallel to vegetational changes have been studied in the field. Older maps, earlier flora lists, and aerial photos

have been used. Particle size is analyzed according to Atterberg (see Ekström 1927). Organic substance is determined as loss on ignition at about 600°C. Soil acidity is given as pH in a suspension of water or 0.2 M KCl in the proportions liquid to soil as 2:1.

As a whole the phytosociology follows the works of Passarge & Hofmann (op.cit.), Géhu & Géhu (op.cit.) and Westhoff & Den Held (op.cit.). The nomenclature of plant communities follows mainly the proposals by Bach et al. (1962) and Rauschert (1963). The Raunkiaer life forms and the Iversen (1936) hydrotypes are taken from Braun-Blanquet (1964), the plant distribution types from Sjörs (1967), see also Böcher (1943 b) and Barkman & Westhoff (1969). Certain concepts and terms are found explained in Westhoff (1951) and Westhoff & Den Held (op.cit.). For vascular plant I have in general followed the nomenclature of Weimarck (1963), for bryophytes Arnell (1956) and Nyholm (1954-69), for lichens Gams (1967) and Poelt (1969). The following works have been used in the determination of the plant material for vascular plants: Neuman & Ahlfvengren (1901), Hylander (1955), Lid (1963), and Garke (1972), for bryophytes Jensen (1939) and Malmer (1966), for lichens Magnusson (1929, 1936), Galløe (1954), Klement (1956/57), Ahti (1961, 1966), and Olsson, H. (1972 b). The nomenclature of soils agrees essentially with Schroeder (1972), see also Kubiëna (op.cit.), Laatsch (1957), Reuter (1956/57), Mückenhausen (1962), Kundler (1965), and Duchafour (1970). The soil colour is determined according to Munsell 1954.

Definitions

anmoor-humus with mineral grains without typical peat formation. The mixture is black or dark grey with very decomposed parts. The organic matter does not exceed 30 %. The humus horizon can reach up to 30 cm (see Kubiëna 1953 pp. 40-41, Duchafour 1970 p. 159).

aue soil—soil type (see Kubiëna op.cit., Schroeder 1972 p. 112) typical in the lowland, e.g., in certain terrain depressions and along rivers. Often the reduction horizon is missing.

bay bar—a bar extending across the mouth of a bay.

beach bar—a bar forming land tongues, often near debouched rivers.

beach ridge—mounded beach materials. Beach ridges may occur singly or as series of deposits.

characteristic taxa—a 'faithful' taxon in a plant community showing floristic qualities, dynamic conditions, and

ecological aspects. Characteristic taxa combination (see Westhoff & Den Held 1969) can be used even where characteristic taxa are missing in a vegetation unit.

companion taxa—taxa occurring equally in several plant communities (Westhoff 1951). Low diagnostic value.

differential taxa—occurring in certain plant communities and missing in others, marking varieties and sub-associations. A differential group of taxa can be used where characteristic taxa are missing in a vegetation unit.

eluvial horizon—leached horizon below the surface soil (see Schroeder 1972).

halophilic—mainly in halinic milieu, e.g., halophilic plants, halophytes. The halinic habitat can be divided according to the salt concentration into oligo-, meso-, and polyhalinic sites (see Iversen 1936). Plants enduring more than 0.5 % salt concentration are said to be halophytes (see Stålfelt 1964).

humus lenses—very small humus layers in the soil profile (see Ranwell 1960 Fig. 6).

illuvial horizon—B-horizon of the soil profile.

podsoloid—in the sense of Linnermark (1960) not developed podsol. In this work used to classify weakly developed podsoles, especially of *Agrostio-Quercetum roboris*, similar to semipodsol in the Kubiëna (op.cit.) soil classification. A stage between podsol and brown earth.

pseudogley—soil type influenced by stagnant water. No oxidation or reduction horizon (see Duchafour 1970, Schroeder 1972).

ranker—weakly developed soil with a small humus layer (A-C-profile) in general on poor silicate sands.

rendzina—weakly developed soil with a small humus layer (A-C-profile) on calcareous ground, with more than 40 % carbonate content. The related *pararendzina* has a carbonate content of 10-40 %. Soils of 10-20 % are related to ranker and called *pararanker* (Schroeder op.cit.).

root layer—many roots and rhizome parts concentrated to a given level in the soil profile (see Ranwell loc.cit.).

sere—the whole series of plant communities developed in a given situation, e.g., halosere, xerosere, and hygrosere. Transitory communities are called seral stages. The sere may be separated into subseres.

subsoil—a layer of the regolith, grading into the surface soil above and into the unmodified bed below. Often without organic matter.

surface soil—the top of the ground, often with organic matter.

syrosem—undeveloped soil, e.g. dune syrosem.

Abbreviations

A—mineral horizon, usually with organic matter, in the surface soil

al—concentration of Al-compounds

ass.nov.—association presented for the first time

auct.—auctorum

B—mineral horizon below A- and E-horizons

Br.-Bl.—Braun-Blanquet

C—characteristic taxon

C—horizon of unaffected soil

comm.nov.—community presented for the first time

D—differential taxon

E—eluvial horizon below A-horizon

em.—revaluation

fe—concentration of Fe-compounds

h—humified decomposed organic matter or humus concentration

L—litter

O—organic horizon above the mineral soil

R.Tx.—R. Tüxen

S—horizon, influenced by stagnant water

SMHI—Sveriges meteorologiska och hydrologiska institut

sub nom.—under the name

var.—variant or variety

vic.—vicariant

Plant communities

At the end of the 19th century Warming started to classify the vegetation on sandy soils, summarized in a work of 1909. Raunkiaer (1914) continued with a phytosociological system from Skagens Odde, northernmost Jutland. In Sweden Erikson (1896) has made a small contribution in accordance with the work of Warming. Nilsson, A. (1902) divided the Swedish vegetation into series: heath series, meadow series and mire series. Under the heath series Nilsson, A. (op.cit. p. 135) also classified sands with acidophytes, e.g. *Corynephorus*-vegetation, as well as basiphytes belonging to steppe-like vegetation. Sjörs (1967) accepted the series concept but added the steppe series including *Antherico - Koelerietum glaucae*. He dealt with the maritime sands apart from the series (op.cit. pp. 89-90, 119, 143-144). Regel (1928) has presented a wide register of plant communities found on sandy soils. Du Rietz, G.E. (1921), Andersson, O. (1950 a) and Tüxen (1951) have made contributions from South and Middle Sweden. Vegetational surveys can also be found in Sterner (1922), Malmer et al. (1965) and Olsson, H. (1971).

South Sweden is phytogeographically a transitional area between Western and Central as well as between Continental and Northern Europe. Therefore it may be illustrative to place the investigation area in a hypothetical quadrant system (Fig. 3). In the middle of the province of Scania a W-E line may be drawn, which divides the province into two parts, a northern and a southern one, mainly following a W-E axis of glaci-fluvial sand (see Lundegårdh et al. 1964 p. 300). Several plant communities common in Central and Continental Europe reach this line and go further to the north only along the Baltic coast, the islands of Öland and Gotland. In the Vomb plain, central Scania, several vegetation units meet and cross. Though the quadrant system is hypothetical the N-S line has points of contact with the *Erica-Narthecium-Ledum* border (Granlund 1925) further to the north, especially on the South Swedish highland. It is continued by the *Erica*

tetralix - *Cynanchum* line further to the south on the European continent (Böcher 1943 b p. 363).

Though certain plant communities could be fragmentary and must be regarded as outposts of the main distribution in Europe, the investigated vegetation represents a totality, a synthesis of floristic and ecological qualities. The descriptions deal with classification, structure, development, ecological remarks, distribution, and sociological relationships. A phytosociological survey of the classification of the South Swedish vegetation is presented in Table 3, the separate plant communities in the Tables I-XX and some ecological notes from the sites in Table XXII. The plant communities are illustrated in the distribution maps 1-36.

Drift vegetation

Annual drift vegetation

Atriplicetum littoralis (Warming 1906) Westhoff & Beeftink 1950 (Table I, distribution map 1)

Classification: *Atriplex littoralis*, *A. calotheca* and *Tripleurospermum maritimum* are characteristic taxa of *Atriplicetum littoralis* and *Atriplicetum littoralis*. *Salsola kali* ssp. *kali* and *Atriplex latifolia* belong to *Cakiletales maritimae* and *Cakiletales maritimae*. The most prominent companion taxa are ranked with *Agropyreteles pungentis* and *Agropyro-Rumicetum crispum*.

Structure: The vegetation consists of a short to medium, open to closed, single-layered, ephemeral plant community with halophytes and nitrophytes, halo-nitrophytes. *Atriplex littoralis* and *A. latifolia* determine the physiognomy with a high degree of cover. *Elymus arenarius* and *Agropyron junceum* are scattered. In certain stands the therophyte *Tripleurospermum maritimum* may be found, especially on sheltered places (see Nordhagen 1940, Dahl & Hadač 1941 p. 291, Tüxen 1950 p. 106, Fröde 1957/58 and Gillner 1960 pp. 90-92). Ardö

Table 3. Vegetation units on sands in South Sweden.

Class	Order	Alliance	Association/Community	Subassociation/Sociation
Cakiletea maritimae	Cakiletalia maritimae	Atriplicion littoralis Salsolo-Honkenyon peploidis	Atriplicetum littoralis Cakiletum maritimae	Cakile maritima soc.
Agropyretea pungentis	Honkenyo-Crambetalia maritimae Agropyretalia pungentis	Honkenyo-Crambion maritimae Agropyron pungentis	Honkenyetum peploidis Honkenyo-Agropyretum acuti Lepidietum latifolii	
Ammophiletea	Elymo-Ammophiletalia arenariae	Ammophilion borealis	Elymo-Ammophiletum	Typical subass. Ammophila arenaria soc. Hieracium umbellatum spp. subass.
Artemisietea vulgaris			Berteroa incana-Elymus arenarius comm.	
Koelerie-Coryne- phoretea	Corynephoretalia	Spergulo-Corynephorion	Cladonio-Corynephoretum	Typical subass. Cladonia subass.
	Festuco-Sedetalia	Galio-Koelerion	Violo-Corynephoretum	Typical subass. Cladonia subass.
		Thero-Airion	Teesdalia-Corynephoretum	Typical subass. Artemisia campestris subass.
		Koelerion glaucae	Pleurozium schreberi- Agrostis tenuis comm. Antherico-Koelerietum glaucae	Typical subass. Cladonia subass.
Molinio-Arrhenatheretea	Arrhenatheretalia	Arrhenatherion elatioris	Festuca ovina-Rumex acetosa comm.	
Nardo-Callunetea	Vaccinio-Genistetalia	Salicion arenariae	Salicetum arenariae	Ammophila arenaria subass. Carex nigra subass. Empetrum nigrum soc. Festuca arenaria subass. Polydium vulgare subass. Lophocolea hetero- phylla subass. Calluna vulgaris soc.
		Empetrium nigri	Salici-Empetretum	
		Cladonio-Callunion Euphorbio-Callunion	Cladonio-Callunetum Agrostio-Callunetum	
Urtico-Sambucetea	Urtico-Crataegetalia	Urtico-Crataegion	Agropyro-Rosetum rugosae	
Betulo-Franguletea	Rubo-Franguletalia	Molinio-Frangulion	Molinio-Myricetum gale	Salix arenaria subass. Molinia coerulea soc.
Vaccinio-Piceetea	Vaccinio-Piceetalia	Cladonio-Pinion	Cladonio-Pinetum sylvestris	Typical subass. Corynephorus canescens subass.
		Vaccinio-Pinion	Vaccinio-Pinetum sylvestris Deschampsia flexuosa-Pinus sylvestris comm.	Empetrum nigrum subass. Quercus petraea subass.
Deschampsio-Quercetea robori-petraeae	Melampyro-Quercetalia	Melampyro-Quercion	Agrostis tenuis-Populus tremula comm. Oxalis acetosella-Quercus petraea comm. Melampyro-Quercetum roboris Calamagrostis epigeios vic.	Typical subass. Corylus avellana subass. Corynephorus cane- scens subass.
		Agrostio-Quercion	Agrostio-Quercetum roboris	
Carici-Alnetea glutinosa	Irido-Alnetalia glutinosae	Irido-Alnion glutinosae	Irido-Alnetum glutinosae	Potentilla palustris subass. Mnium punctatum sub- ass.
Geranio-Fraxinetea	Alno-Fraxinetalia excelsioris	Filipendulo-Fraxinion excelsioris	Filipendulo-Alnetum glutinosae	
Molinio-Betuletea pubescentis	Molinio-Betuletalia pubescentis	Pleurozio-Betulion pubescentis	Myrico-Betuletum pubescentis	
		Sphagno-Betulion pubescentis	Polytricho-Betuletum pubescentis	
			Carex nigra-Calamagrostis epigeios comm.	
Plantaginetea majoris	Plantaginetalia majoris	Agropyro-Rumicion crispi	Carex rostrata-Juncus effusus comm.	
Parvocaricetea	Caricetalia nigrae	Caricion canescentis- nigrae	Caricetum canescentis- nigrae	Carex canescens soc. Sphagnum recurvum subass.
Phragmitetea	Magnocaricetalia	Magnocaricion	Caricetum acutae	Polygonum amphibium subass. Campyllum polygamum subass.
Potametea	Luronio-Potametalia	Potamion graminei	Sparganium minimum comm.	

(1957 p. 42) has reported a plant community where the presence of *Juncus bufonius* is striking and more dominant than the *Atriplex* spp., probably corresponding to a specific subassociation. A floristic composition similar to the *Atriplicetum littoralis* *chenopodietosum* (Tüxen & Böckelmann 1957 p. 187) seems to be lacking on studied sites. The structure of the drift vegetation with the presence of *Festuca arundinacea*, on the island of Hallands Väderö, described by Holmgren (1921 p. 58) indicates a transitional stage between *Atriplicion littoralis* and *Agropyro-Rumicion crisp*i.

Development: The pioneer drift vegetation with eutrophic, strongly halophilic and nitrophilic plant communities is developed where the tang supply is adequate and the wracks do not disappear. The stands are often formed as small zones on the beaches (see Warming 1906 p. 70) separated from other vegetation and only sometimes in contact with *Cakiletum maritimae* and *Honkenyo-Agropyretum acuti*. Plant communities belonging to *Atriplicion littoralis* can be developed into *Agropyrete*a *pungentis* or *Agropyro-Rumicion crisp*i. In South Sweden Turesson (1919), Holmgren (op.cit.), Vallin (1925), Dahlbeck (1945), Gillner (1960) and Tyler (1969) have described plant communities on stable nitrophilic habitats of *Agropyro-Rumicion crisp*i.

Ecological remarks: The wrack ecosystem forms a closed unit with specialized organisms in a nitro-halophilic environment. The productivity in the stands is high. The soil type is a beach syrosem with a tang mixture. Analyses from Dahl & Hadač (loc.cit.) indicate a high tolerance of the salinity. The soil reaction in the rhizosphere seems to vary between 6.5 and 7.5.

Distribution: *Atriplicetum littoralis* occurs along the European west coast from the northern parts of Norway to North France, round the British Isles and in the transitional area between the North Sea and the Baltic Sea (Warming op.cit., Holmgren op.cit., Tüxen 1937, 1950, Christiansen 1938, Nordhagen op.cit., Dahl & Hadač loc.cit., Dahlbeck 1945, Salisbury 1952, Böcher 1952 b, 1969, Ardö loc.cit., Tüxen & Böckelmann loc.cit., Gillner loc.cit., Beef-tink 1965, Jessen 1968, Géhu & Géhu 1969, Westhoff & Den Held 1969, Runge 1973) and along the South Baltic seashores to Poland (Libbert 1940, Fukarek 1961, Passarge 1964, Piotrowska & Celiński 1965, Piotrowska 1966). Of a special kind is

an *Atriplex* spp. drift line on the southern parts of the island of Gotland (Englund 1942 p. 155), probably an outpost to the northern Bothnian drift communities. The *Atriplex glabriuscula* - *Atriplex calotheca* ass. (Fröde 1957/58) represents a position between the Atlantic *Atriplicetum sabulosae* and *Atriplicetum littoralis* in the SE Baltic parts. Within the investigation area *Atriplicetum littoralis* has been found at Tönnersa, Ängelholm and Falsterbo.

Sociological relationships: Only *Atriplicetum littoralis* belongs to *Atriplicion littoralis* (Westhoff & Den Held loc.cit., Géhu & Géhu loc.cit.). Of the five associations separated by Nordhagen (1940) *Atriplicetum littoralis* and *Atriplicetum latifolii* can be included in this alliance. The last association often seems to form a sociation, corresponding to the *Atriplex hastata* (=latifolia) var. *salina* soc. proposed by Géhu & Géhu (loc.cit.). Beef-tink (op.cit.) has distinguished a *Salsola kali* subass. similar to *Atriplex littoralis* - *Salsola kali* ass. (Tüxen 1950). *Matricario maritimae* - *Atriplicetum littoralis* (Tüxen loc.cit.) and *Atriplex glabriuscula* - *Atriplex calotheca* (Fröde op.cit.) are related. *Atriplicion littoralis* is together with *Salsolo-Honkenyon peploidis* ranked with *Cakileta* *maritimae*. A second order of *Cakileta maritimae* is *Thero-Suadetalia* (see Géhu & Géhu op.cit., Westhoff & Den Held op.cit.).

Cakiletum maritimae van Dieren 1934, prov., (Table I, distribution map 2)

Classification: *Cakile maritima* and *Atriplex sabulosa* are characteristic taxa of *Cakiletum maritimae* and *Salsolo-Honkenyon peploidis*. *Salsola kali* ssp. *kali* and *Atriplex latifolia* belong to *Cakileta maritimae* and *Cakileta maritimae*. The most important companion taxa are ranked with *Agropyrete*a *pungentis* and *Ammophileta*. Sometimes a *Cakile maritima* soc. is formed.

Structure: The vegetation consists of a halo-nitrophilic, single-layered plant community with different therophytes. *Cakiletum maritimae* is physiognomically well defined by the succulent *Cakile maritima* and often the thorny, fleshy *Salsola kali* growing together or separate (see Nordhagen 1940, Géhu & Géhu 1969). In general they are clustered. A population of *Cakile maritima* forms dense to closed, intermediate-growing stands, a pioneer sociation. *Salsola kali* grows luxuriantly in stands of *Agropyro-Rumicion* (Nordhagen op.cit. p. 58), not

seen within the investigation area. *Elymus arenarius* and *Ammophila arenaria* appear very scattered in the association.

Development: Often pioneer plant communities occur on the seashores or in the littoral zone on immersed beaches, along estuaries and on the edge of small beach lakes. The habitats are composed of plant residues or organic deposits forming initial or interval plant communities on small elevated fringes in a wet to rather dry milieu. *Cakileum maritima* is normally separated from *Elymo-Ammophiletum* even though *Cakile maritima* soc. could be found on organic material cast up from the sea just near the dune front. In the Atlantic districts *Cakileum maritima* could be in contact with *Elymo-Agropyretum junceiformis*. In South Sweden *Honkenyetum peploidis* can occupy degenerated *Cakileum maritima*. With increased tang supply a vegetational development to *Atriplicetum littoralis* can be seen. In some places, especially along estuaries, also contact with *Agropyro-Rumicion* occurs.

Ecological remarks: Living conditions in the ecosystem are concerned with salinity and instability. The supplied organic material often mixed with fresh aeolian sand forms a milieu most preferable for the plants. Summer annuals with a shallow branchy root system die away in the autumn when the plant community disappears. The soil type is a beach syrosem with a tang mixture. The humus content in the surface soil is about 0.3 % and in the subsoil 0.2 %. The pH is about 6.5 (in KCl 6.0) in the rhizosphere and somewhat higher at 50-60 cm. The grain size varies from fine to coarse.

Distribution: *Cakileum maritima* and similar vegetation seem to occur from Norway to France, round the British Isles and in the SW Baltic districts, scattered or in whole stands (Warming 1906, 1909, van Dieren 1934, Nordhagen op.cit., Böcher 1941, 1952 b, Andersson, O. 1950 a, Raabe 1950, Tüxen 1950, 1967 a, Braun-Blanquet & Tüxen 1952, Salisbury 1952, Ardö 1957, Vanden Berghen 1958, Boerbom 1960, Gimingham 1964 b, Beeftink 1965, Heykena 1965, Wiemann & Domke 1967, Géhu & Géhu op.cit., Westhoff & Den Held 1969). Luxuriant stands from the island of Gotland reported by Englund (1942 p. 95) represent outposts to the north. In South Sweden *Cakileum maritima* can be seen along the coast from Haverdal to Sandhammaren

except at Ängelholm. The absence at Furuboda is a result of the lack of seaweed cast up on the shore. Sometimes *Cakile maritima* can grow ruderaly in the dune system.

Sociological relationships: *Cakileum maritima* is placed into *Salsolo - Honkenyon peploidis* (sub nom. *Salsolo Minuartion peploidis* R.Tx. 1950) and seems to correspond to *Cakileum friscum* (see Tüxen 1950, 1955, Beeftink op.cit., Wiemann & Domke op.cit., Géhu & Géhu op.cit.). Nordhagen (op.cit.) proposed an *Atriplicetum sabulosae* as well as a *Cakileum maritima* belonging to *Atriplicion littoralis*. In Tüxen (1950) several associations are placed into *Salsolo - Honkenyon peploidis* such as *Atriplex glabriuscula - Polygonum Raji* ass., especially located on the British Isles (see Braun-Blanquet & Tüxen op.cit. p. 236, Salisbury op.cit., Gimingham op.cit. pp. 81-84) and *Atriplicetum tornabeni* (= *sabulosae*, *laciniatae*, *arenariae*) described by Nordhagen (op.cit.), Beeftink (op.cit.) and Géhu & Géhu (op.cit.). Also Mertensio- *Atriplicetum arenariae* (Tüxen 1967 a) from southernmost Norway is related. Géhu & Géhu (op.cit.) and Westhoff & Den Held (op.cit.) have separated a *Cakile maritima* soc. from *Atriplicetum sabulosae*. In South Sweden the proposed *Cakile maritima* soc. of *Cakileum maritima* seems to be the only sociation belonging to *Salsolo - Honkenyon peploidis*. In the Atlantic region also *Atriplex glabriuscula* soc., *Salsola kali* soc. (Géhu & Géhu op.cit.), *Honkenya peploides* soc. and *Beta maritima* soc. (Beeftink op.cit.) are registered. *Salsolo - Honkenyon peploidis* is together with *Atriplicion littoralis* ranked with *Cakilealia maritima* belonging to *Cakiletea maritima*.

Perennial drift vegetation

Honkenyetum peploidis auct. (Table II, distribution map 3)

Classification: *Honkenya peploides* is a characteristic dominant of *Honkenyetum peploidis*. *Ammophila arenaria*, *Cakile maritima* and *Salsola kali* ssp. *kali* are differential taxa towards *Honkenyo-Agropyretum acuti* and *Lepidietum latifolii* belonging to *Agropyretalia pungentis* as well as to the inland *Berteroa incana - Elymus arenarius* comm. of *Artemisietea vulgaris*. *Agropyron x acutum* is a differential taxon of a specific variant. *Elymus arenarius*, *Rumex crispus*, *Solanum dulcamara* var.

marinum and *Crambe maritima* are characteristic taxa of high order, *Honkenyo-Crambion maritimae*, *Honkenyo-Crambetalia maritimae* and *Agropyretea pungentis*. The companion taxa, such as *Atriplex littoralis* and *Agropyron repens*, are of less importance. Possibly a *Honkenya peploides* soc. can be distinguished besides the *Agropyron acutum* var.

Structure: The vegetation consists of a halonitrophilic, single-layered plant community totally dominated by the low-growing hemi-cryptophyte *Honkenya peploides*. The stands are formed as green fringes in front of the outer dunes (see Warming 1906 p. 98) or, in a mosaic with other beach vegetation, irregularly as small elevated tufts. On less exposed sites the structure is denser and in some places closed stands are seen. The superterranean shoots are firm and green, different from the pale and moist, subterranean elongated rhizomes.

Development: *Honkenyetum peploidis* is found on rather flat seashores on places where other plants, located on maritime sands, have difficulties in thriving, e.g., annuals from *Cakiletum maritimae* as well as perennials from *Elymo-Ammophiletum*. *Honkenya peploides* can endure certain sand accretion in the position of the upper supralittoral (Sernander 1917 p. 100). The vegetation forms rather stable stands, also describing cycles on the beaches (see Géhu & Géhu 1969 p. 141), on soils influenced by the drifts on both exposed and protected places. The plant community is often in a mosaic with *Cakiletum maritimae*, *Honkenyo-Agropyretum acuti*, *Elymo-Agropyretum junceiformis* or *Elymo-Ammophiletum*. Normally *Honkenyetum peploidis* grows in a separated belt between *Cakiletum maritimae* and *Elymo-Ammophiletum*, according to Fukarek (1961 pp. 88-89) a primary stage in the dune system. The development of *Honkenyetum peploidis* seems to be optimal on sandy gravels, often mixed with shells.

Ecological remarks: The ecosystem is very dependent on the combination of climate and soil hydrology leading to a specific salinity and instability. According to Géhu & Géhu (op.cit. p. 142) the water regime is quite another in *Honkenyetum peploidis* compared with the Atlantic *Elymo-Agropyretum junceiformis*. The soil type is a beach syrosem with a weak tang mixture. Large scattered rhizomes reach 50 cm in the subsoil. The humus content in the surface soil is about 0.2 % and in the

subsoil 0.3 %. The mean value of pH is 7.0 (in KCl 6.5) in the surface soil and 7.4 (6.9) at 50-60 cm. The particle size at Tönnersa consists of both coarse and fine fractions.

Distribution: A vegetation physiognomically determined by *Honkenya peploides* is common from Norway to Portugal, round the British Isles and on several parts in the Baltic districts as well as along the Bothnian Bay shores. *Honkenyetum peploidis* seems to occur from the province of Bohuslän on the Swedish west coast (Friesendahl 1926 p. 126, Hallberg 1971 Table 9) to South France. Several authors have treated this plant community in different ways (Warming loc.cit., Sernander loc.cit., Böcher 1952 b Table 1, Klement 1955 Table 4, Beefink 1965 pp. 136-137, Heyken 1965 pp. 14-21, Géhu 1968, Géhu & Géhu op.cit., Westhoff & Den Held 1969 p. 73). In several parts of the Atlantic region (Tüxen 1937, 1967 a, Christiansen 1938, Westhoff 1947, Braun-Blanquet & Tüxen 1952 p. 229, Tansley 1953, Ardö 1957 p. 43, Tüxen & Böckelmann 1957, Vanden Berghen 1958, Boerbom 1960, Wiemann & Domke 1967, Runge 1973) and along the South Baltic coast (Preuss 1911-12, Libbert 1940, Fukarek op.cit., Piotrowska & Celiński 1965) *Honkenya peploides* is associated with *Elymo-Agropyretum junceiformis* or the south vicariant *Euphorbio-Agropyretum junceiformis*, in certain places in the Baltic region also *Elymo-Ammophiletum*. On Iceland, northern parts of Norway, along the Bothnian Bay shores, round the island of Gotland as well as on the coast of the Baltic States *Honkenya peploides* is ranked with the boreal-Arctic plant communities of *Honkenyo-Elymion peploidis* (Regel 1928, Tomuschat & Ziegenspeck 1929, Lemberg 1933, Kalela 1939 Table 69, Englund 1942 p. 94, Enequist 1944 Fig. 15, Nordhagen 1955, Tüxen 1970 a). Within the investigation area *Honkenyetum peploidis* appears from Haverdal to Falsterbo, also near Trelleborg (Sernander loc.cit.).

Sociological relationships: *Honkenyetum peploidis* is a very specialized association, often regarded a *Honkenya peploides* soc. (Beefink loc.cit.) placed into *Cakiletea maritimae*. Both structure, ecology and morphological adaptation allow closer relationships to *Ammophiletea*, where the combination with *Agropyron junceum* ssp. *boreoatlanticum* is typical but in South Sweden only scattered (see Ardö

loc.cit.). The Arctic and Circumboreal Honkenyo-Elymetum belonging to Honkenyo-Elymetea (Tüxen 1970), studied by the author on the island Sandön in the archipelago of Stockholm (July 1972) and on the island Andøy (July 1969) in North Norway, consists of a halo-nitrophilic plant community very often together with *Lathyrus maritimus*. Potentillo-Elymetum arenariae (Tüxen 1966) belonging to Agropyro-Rumicion on more nitrophilic sites can also contain *Honkenya peploides* (see Dahl & Hadač 1941 p. 302, Hallberg loc.cit. Table 8). Géhu (op.cit.) and Géhu & Géhu (op.cit.) have placed Honkenyetum peploidis into Agropyreteea pungentis, a vicariant class of Honkenyo-Elymetea both with coastal halophilic plant communities. Agropyreteea pungentis includes parts of Agropyro-Rumicion, Convolvulion sepil and Angelicon littoralis. Thus *Honkenya peploides* can be arranged into five separate alliances, viz., Salsolo - Honkenyon peploidis, Agropyro - Honkenyon peploidis, Honkenyo-Elymion, Agropyro - Rumicion crispus and Honkenyo - Crambion maritimae. Studies by Warming (op.cit. p. 81), Friesendahl (loc.cit.), Böcher (1952 b Table 1) and Hallberg (loc.cit.) point to the occurrence of Honkenyo - Crambion maritimae in parts of West Sweden and Denmark. The analyses made by Böcher (loc.cit.) indicate other plant communities characterized by the presence of *Beta maritima* as well as *Crambe maritima* belonging to the same alliance placed into Honkenyo - Crambetalia maritimae of Agropyreteea pungentis.

Honkenyo-Agropyretum acuti R.Tx. 1955 (sub nom. Minuartio-Agropyretum acuti) (Table II, distribution map 4)

Classification: *Agropyron x acutum* is a characteristic taxon of Honkenyo-Agropyretum acuti. *Elymus arenarius*, *Honkenya peploides*, *Solanum dulcamara* var. *marinum* and *Rumex crispus* are of high order, *Agropyron pungentis*, *Agropyretalia pungentis* and *Agropyreteea pungentis*. *Ammophila x baltica* and *Agropyron repens* are among the companion taxa. The dominance of *Elymus arenarius* is an indication of a specific variant (Géhu & Géhu 1969 p. 149).

Structure: The vegetation consists of a dense to closed, single-layered, halo-nitrophilic plant community. In South Sweden *Elymus arenarius* is totally dominating and often about one metre high. Both

Honkenya peploides and *Agropyron x acutum* have an elongated growth. On an offshore barrier island south of Copenhagen (Gravesen & Vestergaard 1969 pp. 69-70) a corresponding vegetation is more open and rich in species.

Development: Honkenyo-Agropyretum acuti occurs where the seaweeds, that have been cast up, can be transported landwards forming a rather instable habitat of perennial drift vegetation. If the decomposition of drift organic matter is too rapid, *Cakiletum maritimae* or *Atriplicetum littoralis* develops, if slow, Honkenyo-Agropyretum acuti or *Lepidietum latifolii*. In stronger nitrophilic habitats *Agropyron pungentis* is replaced by *Agropyro-Rumicion crispus* (see Böcher 1952 b, Jessen 1968, Gravesen & Vestergaard op.cit.). Plant communities belonging to these two alliances decrease if the drift supply is stopped.

Ecological remarks: The ecosystem is dependent on a specific drift supply and microclimate on rather protected habitats. The soil type is a syrosem with a tang mixture. The humus content in the surface soil is about 0.3 %, in the subsoil 0.7 %. The increase is an effect of undecomposed plant residues. The pH is 6.6 (in KCl 5.7) in the surface soil and 7.5 (KCl 7.1) in the subsoil.

Distribution: Plant communities belonging to Agropyretalia pungentis have a Mediterranean-Atlantic range (Géhu & Géhu loc.cit.) and normally cover the whole littoral. Honkenyo-Agropyretum acuti (Tüxen 1955, Géhu 1968, Géhu & Géhu loc.cit., Runge 1973 p. 39) seems to have a northern outpost at Falsterbo as well as south of Copenhagen (Gravesen & Vestergaard loc.cit.).

Sociological relationships: A proposal to place Honkenyo-Agropyretum acuti into Agropyro-Rumicion crispus by Tüxen (1955) has been followed in classifications by Géhu (op.cit.), and Géhu & Géhu (op.cit.) into Agropyron pungentis as well as by Runge (loc.cit.) into Agropyro-Honkenyon peploidis. A related plant community is Atriplici-Agropyretum pungentis (see Beefink 1965) occurring from Denmark to France. In South Norway different Elymus-communities have been classified into Agropyro-Rumicion (Størmer 1938 Table 4, Nordhagen 1940 pp. 94-96, Dahl & Hadač 1941 Table 7). Iversen (1936 Table 28) and Böcher (loc.cit.) point out the affinity of *Elymus arenarius* for

nitrophilic plant communities. Honkenyo- Elymetum arenariae (Tüxen 1970) is a northern substitute of Honkenyo- Agropyretum acuti which is regarded a vicariant, on sheltered places, of the Atlantic Elymo- Agropyretum junceiformis.

Lepidietum latifolii auct. (Table II, distribution map 5)

Classification: *Lepidium latifolium* is a characteristic taxon, also a dominant, of *Lepidietum latifolii*. *Galium verum*, *G. aparine*, *Bromus hordeaceus* ssp. *hordeaceus* and *Linaria vulgaris* are differential taxa towards Honkenyetum peploidis and Honkenyo- Agropyretum acuti of Agropyreteea pungentis as well as towards Berteroa incana- Elymus arenarius comm. of Artemisietea vulgaris. *Elymus arenarius*, *Rumex crispus* and *Solanum dulcamara* var. *marinum* are of high order, Agropyrion pungentis, Agropyretalia pungentis and Agropyreteea pungentis. Agropyron repens is a prominent companion taxon, according to Dahlbeck (1945 p. 63) a subdominant.

Structure: The vegetation consists of a weakly halonitrophilic, single-layered plant community with open to closed stands, physiognomically determined by *Lepidium latifolium* (see Raabe 1950). Different hemicryptophytes of low degree of cover are present. The number and the frequency of plants are strongly variable.

Development: *Lepidietum latifolii* forms a rather stable plant community on the upper seashore drift lines as well as on the plain sand. The association is in contact with Honkenyo- Agropyretum acuti, a more instable plant community, on more nitrophilic places also with plant communities of Agropyro- Rumicion crisp. Stands of *Lepidium latifolium* seem to be natural along the coast though ruderal plants on certain sites could be found (Dahlbeck loc.cit.).

Ecological remarks: The ecosystem is dependent on meso- to oligohalinic, often rather dry habitats. According to Dahlbeck (loc.cit.) a drift layer of varying thickness on the mineral soil, a type of syrosem, is often present.

Distribution: The range of *Lepidietum latifolii* is mainly the same as of Honkenyo- Agropyretum acuti, Mediterranean-Atlantic (Géhu 1968, Géhu & Géhu 1969, Westhoff & Den Held 1969), and with a northern outpost at Falsterbo (Dahlbeck loc.cit.).

Sociological relationships: Raabe (op.cit.) has

placed a *Lepidium latifolium* comm. into Agropyro- Rumicion crisp, Westhoff & Den Held (op.cit.) into Angelicon litoralis of Artemisietea vulgaris. Géhu & Géhu (op.cit.) have placed *Lepidietum latifolii* into Agropyrion pungentis of Agropyreteea pungentis.

Marram and sandy grassland vegetation

Marram grass vegetation

Elymo-Ammophiletum (Warming 1909) Br.-Bl. et De Leeuw 1936 em. R.Tx. 1952 (Table III, distribution map 6)

Classification: *Ammophila arenaria* is a characteristic taxon of *Elymo-Ammophiletum* and *Ammophilon borealis*. *Elymus arenarius*, *Lathyrus maritimus* and *Petasites spurius* are differential taxa of *Elymo-Ammophiletum*. A division is made into one *Ammophila arenaria* soc. and two subassociations, a typical one lacking differential taxa and a *Hieracium umbellatum* ssp. subass. including *Festuca arenaria*, *Corynephorus canescens*, *Hieracium umbellatum* ssp., *Carex arenaria*, *Ceratodon purpureus*, *Viola tricolor* ssp. *curtisii* and *Jasione montana* var. *littoralis*. Two taxa, *Salsola kali* ssp. *kali* and *Agropyron repens*, belong to a *Salsola kali* ssp. *kali* variant of the typical subassociation, *Agropyron repens* also to a specific



Fig. 7. *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass. Sandhammaren 1953. Photo H. Weimarck, Skånes Naturskyddsför. Arkiv.

variant of *Hieracium umbellatum* ssp. subass. *Ammophila x baltica*, *Agropyron junceum* ssp. *boreoatlanticum* and *Eryngium maritimum* are ranked with *Elymo-Ammophiletalia arenariae* and *Ammophiletea*. The companion taxa are among *Cakiletea maritimae*, *Agropyretea pungentis* and *Koelerio-Coryneporetea*. Furthermore, there are different cryptogams such as *Cladonia* spp., *Parmelia physodes*, *Dicranum scoparium* and *Pohlia nutans* among the *Hieracium umbellatum* ssp. subass.

Structure: The vegetation consists of a pioneer single-layered or weakly double-layered plant community with open mobile or fixed closed primary or secondary stands on the epilittoral. The stands of the typical subassociation are vital, monotonous in physiognomy and poor in species, sometimes forming only a dense *Ammophila arenaria* soc. (see Tansley 1953 p. 848, Géhu & Géhu 1969 p. 156), e.g., some ruderal therophytes from *Cakiletea maritimae*. At Sandhammaren there are patches of *Salsola kali* together with scarcely spread dune grasses in clustered tufts, forming small embryo dunes. This vegetation with relicts from *Cakiletea maritimae* is rather different from the normal conditions of *Elymo-Ammophiletum*. The structural composition is different from *Agropyretum boreoatlanticum salsolitosum* (Tüxen 1937 p. 14, Piotrowska & Celiński 1965 pp. 131-133) and *Elymeto-Ammophiletum Honkenya peploides* subass. (Libbert 1940 p. 10), where the frequencies of *Agropyron junceum* ssp. *boreoatlanticum* and *Honkenya peploides* are minute. In the typical subassociation clones of *Ammophila arenaria* are separated from clones of *Elymus arenarius* and of *Ammophila x baltica*. Especially at Sandhammaren large tufts of the latter plant grow close to the beach, which is rather different from the opposite side of the Baltic Sea (Fukarek 1961 p. 97) as well as the Swedish west coast, where *Ammophila x baltica* prefers *Hieracium umbellatum* ssp. subass. but compared with *A. arenaria* is less common. *Elymus arenarius* is prominent and somewhere reduced to the typical subassociation.

The physiognomy of *Hieracium* ssp. subass. is strongly changed as a consequence of the debility of the tall dune grasses indicated by an accumulation of undecomposed shoots leading to closer stands. The colour has been altered from green to gray. Somewhere small openings in the vegetation are

colonized by *Corynephorus canescens*. Both *Hieracium umbellatum* ssp. and *Festuca arenaria* are striking and in certain stands of a rather high degree of cover and thus valuable indicators of the condition of this subassociation. Certain xerophytes and termophytes such as *Carex arenaria*, *Jasione montana* var. *littoralis* and *Viola tricolor* ssp. *curtisii* are present but of secondary structural importance. *Petasites spurius* found in Baltic stands can effectively cover the ground (see Preuss 1911-12 p. 60, Steffen 1931 p. 260). *Lathyrus maritimus* can form very closed stands (see Andersson, O. 1950 Table 1) along the coast from Falsterbo to Furuboda, changing the microclimate from dry to hygric in the bottom layer favouring the mosses, especially *Ceratodon purpureus*. With the entrance of this pioneer moss the vegetation is stratified into two layers. On places with reduced sand accretion as at Ängelholm also nitrophytes as *Agropyron repens* can be mixed with the tall dune grasses.

Development: *Elymo-Ammophiletum* is a plant community often in succession after *Elymo-Agropyretum junceiformis* in the Atlantic region or as in South Sweden a pioneer vegetation on mobile maritime sands on the supralittoral. The decreased salinity in the Baltic Sea leads to a dying away of *Elymo-Agropyretum junceiformis* in the Baltic districts (see Libbert op.cit. p. 8, Fukarek op.cit. p. 96, Passarge 1964). The author is of the opinion that *Agropyron junceum* ssp. *boreoatlanticum* within the investigation area grows only in initial stands of *Elymo-Ammophiletum*, as can be seen at Falsterbo or scattered in *Honkenyetum peploidis* shown by Ardö (1957 p. 43). In mesohalinic habitats *Ammophila arenaria* establishes and reaches in the primary stage a maximal vegetative development influenced by continuous sand accretion and flowers when the dunes reach maximal height. In this stage, the optimal phase, several plants are assembled also continuing in the degeneration phase where the sand accretion has nearly ceased. *Elymus arenarius* seems to settle before *Ammophila arenaria* on the foredunes in front of the beach. The marram grass has an extensive horizontal root system on the low primary dunes; in older parts of the dune system it is much closer with big shoots and broad leaves and has increased the ability to bind sand (Westhoff 1947 p. 72). Of the two xerophytes, *Ammophila arenaria* and *Elymus arenarius*, the latter is less effective in binding sand. In general the spread of

Ammophila arenaria takes place by vegetative emerging etages in the sand. Older rhizomes disappear and are replaced by newer ones near the surface induced by the sand accretion.

Elymo-Ammophiletum may be in contact with a *Cakile maritima* soc. or *Honkenyetum peploidis*. A development of *Hieracium umbellatum* ssp. subass. leads normally to a contact with *Violo-Corynephorum*, on certain places directly with *Salici-Empetretum Polypodium vulgare* subass. On places with reduced sand accretion Elymo-Ammophiletum may be transformed into a *Pleurozium schreberi* - *Agrostis tenuis* comm., as at Ängelholm and at Furuboda. On lee slopes *Agrostis tenuis* - *Populus tremula* comm. may border on Elymo-Ammophiletum, which in some places on the dunes may be in contact with *Salicetum arenariae* and *Agropyro-Rosetum rugosae*.

Ecological remarks: The ecosystem with rapidly growing tall dune grasses is dependent on the sand accretion and is registered on mobile as well as on semi-fixed dunes (see Tansley loc.cit., Ranwell 1960 p. 119, Gimingham 1964 b pp. 95-98). The soil type is a dune syrosem with a very thin A-horizon in the *Hieracium umbellatum* ssp. subass. The sand is brown or white. The soil profile contains several humus lenses, root layers and solitary deep rhizomes (Table XXII). The humus content of the typical sub-association is about 0.2 %, increased to 0.3 % in *Hieracium umbellatum* ssp. subass. in the surface soil, in the subsoil below 0.2 %. Parallel to an increase in organic matter there is a decrease in pH. The pH values in the soil profiles have been changed from 6.2 (in KCl 5.4) to 5.6 (4.5) in the surface soil, 6.8 (6.0) to 6.3 (5.2) in the subsoil. Within the area of *Ammophilon borealis* the pH-amplitude is 5.0-9.0 (see Wiemann & Domke 1967). As a whole the grain size can be divided into two fractions, about 80 % > 0.2 mm.

Distribution: Marram grass communities occur along the Baltic, Atlantic, Mediterranean and Pontic coasts. *Ammophilon borealis* reaches from France and British Isles to South Norway and Baltic States, fragmentarily up to South Finland. The transition between the thermophilic Occidental *Euphorbio-Ammophiletum* (Lebrun et al. 1949, Braun-Blanquet & Tüxen 1952, Tansley loc.cit., Vanden Berghen 1958, Géhu & Géhu op.cit., Westhoff & Den Held 1969) and the northern Elymo-Ammophiletum lies

in the southern parts of the Netherlands and the British Isles. Several work treat Elymo-Ammophiletum both on the European west coast (Warming 1909, Raunkiaer 1914, van Dieren 1934, Iversen 1936, Tüxen 1937, 1967 a, 1967 c, Christiansen 1938, Böcher 1941 b, 1945, 1952 a, 1969, Westhoff loc.cit., Salisbury 1952, Tansley loc.cit., Klement 1955, Ardö op.cit., Tüxen & Böckelmann 1957, Willis et al. 1959, Boerbom 1960, Ranwell op.cit., Gimingham op.cit., van der Maarel & Westhoff 1964, Heykena 1965, Wiemann & Domke 1967, Géhu & Géhu op.cit., Westhoff & Den Held op.cit., Runge 1973) and in the Baltic region (Erikson 1896, Nilsson, A. 1901, Hesselman 1908, Warming op.cit., Preuss op.cit., Norlind 1913, Regel 1928, Tomuschat & Ziegenspeck 1929, Steffen loc.cit., Hueck 1932, Libbert loc.cit., Andersson, O. 1950 a, Raabe 1950, Paul 1953, Voderberg 1955, Pettersson 1958, 1965, Fröde 1957-58, Fukarek op.cit., Passarge 1964, Wojterski 1964 a, Piotrowska & Celiński loc.cit., Piotrowska 1966, Ljungberg & Persson, Y. 1973). Elymo-Ammophiletum meets further to the north plant communities of *Honkenyo-Elymetea* as in the East Baltic districts and along the Bothnian Bay as well as the north coast of Norway (Lemberg 1933, Kalela 1939, Enequist 1944, Nordhagen 1955, Tüxen 1970). Of a very special kind is a plant community with *Calamagrostis epigeios* and *C. neglecta* from the seashores of the lake Vänern (see Norén 1906). On Jutland there is an *Ammophila arenaria* soc. with or without *Corynephorus canescens* (Böcher 1941 a Table 12); rarely on certain inland sands. In South Sweden Elymo-Ammophiletum occurs on all studied maritime sands, at Vitemölla only the typical sub-association. The *Ammophila arenaria* soc. is found on several places in the dune landscapes, especially at Haverdal, Tönnersa, Sandhammaren and Furuboda.

Sociological relationships: In 1947 Westhoff (op.cit.) pointed out that an Elymeto-Ammophiletum could be divided into two regional groups, Elymeto-Ammophiletum austrino-atlanticum from Portugal to the island of Texel in the Netherlands and Elymeto baltico-atlanticum northwards on the Atlantic and Baltic sand dunes. The first association was named *Euphorbio-Ammophiletum arenariae* (Braun-Blanquet & Tüxen op.cit. pp. 251-254). The second association, split into a typical subassociation and a *Festuca arenaria* subass. (Tüxen 1937 p.

15), has according to Fukarek (op.cit. p. 108) an area of distribution in the North Sea and the western Baltic Sea. In the East Baltic region Fukarek (loc.cit.) proposed an Elymo-Ammophiletum oriento-balticum with a typical subassociation and an *Artemisia campestris* subass. All the three provincial associations were included in a regional association with a specific *Hieracium umbellatum* subass. group. Wiemann & Domke (op.cit. pp. 276-277) have completed the division of the transitional area between North Sea and western Baltic Sea and proposed an Elymo-Ammophiletum baltico-atlanticum occidentale (North Sea) and an Elymo-Ammophiletum baltico-atlanticum orientale (W Baltic Sea). Tüxen (1967 a p. 249) has separated Elymo-Ammophiletum into two vicariant regional associations, a western *Soncho (arvensis)* -Ammophiletum and an eastern *Petasito (tomentosi)* -Ammophiletum. Géhu (comm. at a Colloque in Paris 1971) has suggested four vicariant associations, viz., *Petasito*-Ammophiletum, Elymo-Ammophiletum, *Lathyro*-Ammophiletum and *Soncho*-Ammophiletum. The first East Baltic association seems to have very small relicts at Sandhammaren and Vitemölla, the third *Lathyro*-Ammophiletum probably related to Elymo-Ammophiletum baltico-atlanticum orientale is rather frequent in some places at Falsterbo but fragments seem to occur from Sandhammaren to Furuboda (see Andersson, O. op.cit. p. 153) along the Baltic coast. On the Swedish west coast Elymo-Ammophiletum is predominant. *Soncho*-Ammophiletum with a western distribution and probably related to Elymo-Ammophiletum baltico-atlanticum occidentale does not seem to occur in Sweden.

Elymo-Ammophiletum has also been classified into primary and secondary units (see Wiemann & Domke op.cit. Faltblatt 7 Table 11). Van Dieren (op.cit. p. 203) has given an Ammophiletum arenariae redivivum also with a *Festuca arenaria* subass. and of a secondary origin. Westhoff & Den Held (op.cit. p. 103) has regarded the secondary vegetation as a specific subassociation, Elymo-Ammophiletum redivivum, sometimes formed as *Ammophila arenaria* soc. Elymo-Ammophiletum belongs to *Ammophilion borealis* (Tüxen 1955 p. 163) together with *Agropyron Honkenion peploidis*, changed to *Agropyron boreoatlanticum* by Géhu & Géhu (op.cit.), placed into *Elymetalia arenarii* (see Tüxen 1955, Westhoff & Den Held loc.cit.). Doing

(1963) has changed the name of the order to Ammophiletalia arenariae and Géhu & Géhu (op.cit.) to Elymo-Ammophiletalia arenariae. Ammophiletea includes, according to Géhu & Géhu (op.cit.), three orders, viz., the northern Elymo-Ammophiletalia arenariae, the Occidental Euphorbio-Ammophiletalia and the Pontic-Mediterranean Ammophiletalia arundinaceae.

Inland lyme grass vegetation

Berteroa incana - *Elymus arenarius* community comm. nov. (Table II, distribution map 7)

Classification: *Berteroa incana* is a local characteristic taxon of the *Berteroa incana* - *Elymus arenarius* comm. *Polygonum amphibium*, *P. convolvulus* and *Brachythecium rutabulum* are differential taxa of the community. *Elymus arenarius*, *Agropyron repens* and *Festuca rubra* are among the companion taxa, the first one also a dominant. The plant community seems to belong to *Artemisietea vulgaris*.

Structure: The vegetation consists of a single-layered or weakly double-layered, open to very closed, plant community. The physiognomy is determined by *Elymus arenarius* together with different hemicryptophytes and geophytes variable in frequency and degree of cover, as *Urtica dioica* and *Berteroa incana*. *Anchusa officinalis* can be found on stands located in dry habitats. The structure of this strongly anthropogenous vegetation differs from a related *Elymus arenarius* comm. in East Scania on dry sand fields (see Andersson, O. & Waldheim 1946 Pl. V) often with *Festuco-Sedetalia* spp. and similar to an *Elymetum arenariae* described from Poland and the Baltic States (see Juraszek 1927 p. 597, Kobendza 1930 Table 6, Steffen 1931 p. 281). However, the combination of *Berteroa incana* and *Elymus arenarius* may be found on more ruderal sites as near the village of Kivik.

Development: The plant community occurs on dry, poor inland sands often in contact with the short dry grassland of *Koelerio-Corynephoretea*. Certain stands are of anthropochorous origin (see Sernander 1915 p. 451, Weimarck 1940 p. 189), along roads or in military training camps. *Elymus arenarius* in the inland can also be a relict (see Steffen loc.cit., Tüxen 1970 p. 265, Hultén 1971).

Ecological remarks: The most important criterion of the ecosystem seems to be the human influence and

the nitrophilic tendency. The soil type is possibly a ranker.

Distribution: The range of *Berteroa incana* - *Elymus arenarius* comm. is very disperse. An inland *Elymus arenarius* comm. has been reported by Juraszek (loc.cit.), Kobendza (loc.cit.), Steffen (loc.cit.), Almqvist (1929 p. 239) and Tüxen (op.cit. p. 281). Within the investigation area the plant community has been registered at Silvåkra in the Vomb plain and at Vitaby in East Scania.

Sociological relationships: In Olsson (1971) an *Agropyron repens* - *Brachythecium rutabulum* comm. was provisionally placed into *Agropyrum*. A new interpretation has shown closer relationship with *Artemisietea vulgaris* and the plant community has been changed into *Berteroa incana* - *Elymus arenarius* comm.

Short dry grassland vegetation

Cladonio (dstrictae) - Corynephorum Krieger 1937 em. Böcher 1941, prov., (Table IV, distribution map 8)

Classification: *Cladonia dstricta* and *Stereocaulon condensatum* are characteristic taxa of *Cladonio-Corynephorum*, *Spergulo-Corynephorion*, and *Corynephoralia*. *Corynephorus canescens* is often a dominant in a typical subassociation, often a sociation. *Cladonia arbuscula et mitis*, *C. chlorophaea* coll., *C. impexa*, *C. cornuta et gracilis*, *C. floerkeana*, *C. pleurota* and *C. uncialis* are differential taxa of a *Cladonia* subass. *Cetraria crispa* and *C. islandica* are found in a *C. crispa* variant. Several taxa are ranked with *Koelerio-Corynephoretea* as *Corynephorus canescens*, *Carex arenaria*, *Cornicularia aculeata*, *Festuca polesica*, *Ceratodon purpureus*, *Cladonia alcicornis*, *Polytrichum piliferum*, *Koeleria glauca*, *Festuca arenaria*, *Viola canina* var. *dunensis*, *V. tricolor* ssp. *curtisi*, *Cladonia furcata*, *Rhacomitrium canescens*, *Jasione montana* var. *littoralis*, *Hieracium umbellatum* sspp. and *Rumex tenuifolius*. Prominent companion taxa are *Ammophila arenaria*, *Dicranum scoparium*, *Parmelia physodes* and *Cephaloziella* sp.

Structure: The vegetation consists of a poor, single or double-layered pioneer plant community with open to closed low-growing stands, physiognomically determined by *Corynephorus canescens*, in the typical subassociation of high vitality. Other plants

are there of secondary importance and a bottom layer is lacking. In the *Cladonia* subass. the surface of the sand is covered by lichen cushions, in some stands dominated by *Cladonia arbuscula et mitis*, in others by *C. impexa*. The lichen luxuriance can change the structure to a cryptogamic community similar to a *Cladonietum mitis* (Krieger 1937) or a *Cladonietum dstrictae* (Langerfeldt 1939). Also *Cladonia uncialis* forms a specific plant community. Together with *Cladonia* spp. *Cornicularia aculeata* is predominant, also shown by analyses made by Tüxen (1928, 1958), Krieger (op.cit.), Langerfeldt (op.cit.) and Böcher (1941 a, 1941 b). The decrease of *Corynephorus canescens* and the increase of *Carex arenaria* in the often very closed stands of *Cetraria crispa* variant are obvious. The dominance of *Carex arenaria* can be striking but the stands are very unlike Thero-Airion plant communities with a pronounced moss layer, as the studied *Pleurozium schreberi* - *Agrostis tenuis* comm. A vegetation with *Agrostis canina* ssp. *montana* (see Stoutjesdijk 1959 Table 6) may be regarded a subassociation (Tüxen 1937 p. 55, Westhoff & Den Held 1969 p. 148) including *Rumex tenuifolius*, *Festuca ovina* and *Hypochoeris radicata*, missing in *Cladonio-Corynephorum* in South Sweden. The given plants are placed into *Teesdalia-Corynephorum*.

Development: *Cladonio-Corynephorum* colonizes dry non-calcareous soil, poor in minerals and with a small humus layer, on eroded aeolian sands. *Corynephorus canescens* can endure a certain sand accretion (Marshall 1967), which is even necessary to keep the plant in a state of high vigour. In very closed *Cladonia* mats the debility of *Corynephorus canescens* is obvious.

The decline in vigour is a failure of development of new adventitious roots (Marshall op.cit.). Rychnovská-Soudková (1961) has suggested that decreased aeration due to the accumulation of humus could be a limiting factor for *Corynephorus canescens* with its high rate of root respiration. Compared with *Ammophila arenaria* the ability of *Corynephorus canescens* to stop blown sand is strongly reduced although the etage growth is rather similar to that of marram grass. Stoutjesdijk (op.cit. p. 36) has reported that under certain instable conditions *Corynephorus canescens* can form small dunes, about one metre in height. The successional stages are manifold. Either one of the mosses *Polytrichum piliferum* and *Ceratodon purpureus* as

pioneers bind the sand through their rhizoids (see Leach 1931 p. 100, Birse et al. 1957) after which the lichens immigrate using the mosses as a foothold. Certain lichens grow on the soil in conjunction with mosses as well as on grass debris (see Alvin 1960 p. 333). Pettersson (1965) has noticed in deflations of the inland dunes of the island Gotska Sandön crustaceous lichens especially *Lecidea* spp. and *Stereocaulon condensatum* accompanied by crusts of bryophytes succeeded by *Cladonia* spp.

Cladonio-Corynephoretum may in some place diffusely border *Violo-Corynephoretum* and on places near the seashores a *Cladonia* subass. of both associations may be present (see Fukarek 1961 p. 115) and possibly related to a *Corynephoretum maritimum* (see Tüxen 1967 a). As a rule *Cladonio-Corynephoretum* is located on the inner coastal dune landscapes especially at Sandhammaren, often in contact with a *Calluna vulgaris* soc., *Cladonio-Pinetum sylvestris*, *Vaccinio-Pinetum sylvestris* and *Melampyro-Quercetum roboris*. The plant community is the first stage, binding the naked sand, in a vegetational succession towards a forest. The development from *Cladonio-Corynephoretum* via a *Calluna vulgaris* soc. to *Melampyro-Quercetum roboris* can be compared to a similar one in the NW Europe from *Spergulo-Corynephoretum* via *Genisto-Callunetum* to an oak-birch forest (see Tüxen 1928 p. 89, Westhoff & Den Held 1969 p. 149).

Ecological remarks: The ecosystem is characterized by the specialized pioneer *Corynephorus canescens* with super- and subterranean organs adapted to blown sand habitats. The soil type is a ranker-dune syrosem, where 10-20 cm of the dark humus layer are filled with masses of small roots, making infiltration of the precipitation water difficult. The C-horizon consists of a yellowish light sand. The stratification is variable (see Stoutjesdijk op.cit., Berger-Landefeldt & Sukopp 1965 p. 45). The humus content, as a rule very low in the typical sub-association, is about 0.5 % in the surface soil and less than 0.2 % in the subsoil. The reaction is very acid. The mean value of pH is 4.9 (in KCl 3.8) in the surface soil and 5.6 (4.6) in the subsoil. The optimal value is pH 5 (Berger-Landefeldt & Sukopp op.cit. p. 51); pH 3.5 (Krieger op.cit.) seems to be the minimum and pH 6.8 (Hohenester 1960 p. 39) seems to be in maximum. The grain size is about 80 % > 0.2 mm.

Distribution: The poor pioneer *Corynephorus canescens* vegetation, in this work called *Cladonio-Corynephoretum*, has an Atlantic to sub-Atlantic area in the Middle or Western Europe with optimum in North Germany (Tüxen 1928, 1937, 1958, 1967 b, Libbert 1932, Krieger op.cit., Langerfeldt op.cit., Böcher 1941 a, 1941 b, 1952, Lebrun et al. 1949, Klement 1955, Stoutjesdijk op.cit., Passarge 1960 p. 144, Berger-Landefeldt & Sukopp op.cit., Krausch 1968 a, Westhoff & Den Held 1969, Klemm 1970 Table 33, *Cladonia mitis* var., Runge 1973). A plant community representing a transitional stage between *Corynephoretalia* and *Festuco-Sedetalia* has been reported by Kobendza (1930), Volk (1931), Kornas (1957), Oberdorfer (1957), Hohenester (1960, 1967), Rychnovská-Soudková (1961) and Passarge (1964). Outposts to the north on the islands of Öland and Gotska Sandön are registered by Arwidsson (1938), Sjögren (1957) and Pettersson (1965). Within the investigation area *Cladonio-Corynephoretum* is found at Ängelholm, Sandhammaren and Furuboda possibly also at Falsterbo but seems to be absent in the Vomb plain.

Sociological relationships: *Cladonio-Corynephoretum* is in South Sweden and Denmark (Böcher op.cit.) a substitute for *Spergulo-Corynephoretum* (Tüxen 1928, 1937, 1955, Libbert 1932, Passarge 1960). The association has been separated in several ways. The lichen-dominated *Corynephorus*-vegetation has been classified as *Cladonieto-Cornicularietum* (Tüxen 1928), *Cladonietum destrictae* (Langerfeldt op.cit.) and *Cladonietum mitis* (Krieger op.cit.). Tüxen (1937), Lebrun et al. (op.cit. p. 149) and Passarge (1960, Hohenester 1967) have used a *Cladonia* subass. Krausch (op.cit.) and Westhoff & Den Held (1969) have regarded the lichen state only a variant of different sub-associations. *Cladonio-Corynephoretum* belongs to *Spergulo-Corynephorion* (Passarge 1960). Passarge (1964), Oberdorfer et al. (1967) and Krausch (op.cit.) have included elements from *Thero-Airion* and *Galio-Koelerion* in *Corynephoretalia* instead of *Festuco-Sedetalia*. Tüxen (1955, 1967 b) has suggested a class *Corynephoretea canescentis* including *Spergulo-Corynephoretum* and *Violo-Corynephoretum* the latter also called *Corynephoretum maritimum* (see Runge 1973 p. 41). A revision made by Krausch (1968) has led to a class named *Sedo-*

Scleranthetea in which *Corynephorus canescens* is only a characteristic taxon of *Corynephoretalia*. But the very broad amplitude of *Corynephorus canescens* with high frequencies also in *Festuco-Sedetalia* indicates a characteristic taxon of high rank of the whole class *Koelerio-Corynephoretea*.

Violo-Corynephoretum Westhoff (1943) 1947 (Table V, distribution map 9)

Classification: *Viola canina* var. *dunensis* is a characteristic taxon of *Violo-Corynephoretum* (Westhoff & Den Held 1969 p. 154). A division is made into a typical subassociation, negatively characterized, and a *Cladonia* subass. with *Cladonia arbuscula* et *mitis*, *C. cornuta* et *gracilis*, *C. impexa*, *C. floerkeana*, *C. pleurota* and *Dicranum scoparium* as differential taxa. One specific variant has been distinguished with *Helichrysum arenarium*, *Thymus serpyllum*, *Dianthus arenarius* and *Rhacomitrium canescens*, also taxa of high order. *Hieracium umbellatum* ssp., *Jasione montana* var. *littoralis*, *Festuca arenaria* and *Viola tricolor* ssp. *curtisii* are characteristic taxa of *Galio-Koelerion* (syn. *Koelerion albescentis*). Several taxa are of high order and ranked with *Festuco-Sedetalia* and *Koelerio-Corynephoretea* as *Corynephorus canescens*, *Carex arenaria*, *Cornicularia aculeata*, *Ceratodon purpureus*, *Cladonia furcata*, *C. alcicornis*, *Polytrichum piliferum*, *Festuca polesica*, *Koeleria glauca*, *Brachytecium albicans*, *Rumex tenuifolius*, *Hypnum cupressiforme* var. *lacunosum*, *Trifolium campestre*, *Tortula ruralis* var. *ruraliformis* and *Teesdalia nudicaulis*. The companion taxa are from *Ammophiletea*, *Festuco-Brometea* and *Nardo-Callunetea*, also various cryptogams such as *Cladonia* spp., *Parmelia physodes*, *Pohlia nutans* and *Cephaloziella* sp.

Structure: The vegetation consists of an open to dense, ephemeral mainly single-layered plant community rich in hemicryptophytes and therophytes. Apart from many xerophytes marked with a shallow root system also certain mesophytes may be present as *Viola canina* var. *dunensis* and *Hypochoeris radicata* (see Iversen 1936 Table 55). Coastal forms, ecotypes, often hairy and with a prostrate growth or rosette plants such as *Jasione montana* var. *littoralis*, cushion mosses and bushy lichens are of structural importance. Westhoff (1947 p. 87) has pointed out the occurrence of *Parmelia physodes*, *Evernia*

prunastri, *Usnea hirta* and *Cetraria glauca* (see in section The Flora under *Parmelia*) specific for the plant community. Different graminids are prominent. In normal succession *Ammophila arenaria* is still present. Of interest is a weak change in aspect: *Viola tricolor* ssp. *curtisii* flowering in late spring, *Galium verum*, *Hieracium umbellatum* ssp., *Jasione montana* var. *littoralis* flowering in summer. The graminids and the cryptogams are common throughout the year. Westhoff (loc.cit.) has found a good homogenousness in the association but this is not valid for the fragments of South Sweden where the number of taxa and degree of cover vary from stand to stand, e.g., the quantity of *Carex arenaria* increased with reduced sand accretion. *Violo-Corynephoretum* consists of various plants also found in *Antherico-Koelerietum glaucae* and *Cladonio-Corynephoretum*. All the three associations have been combined into a *Cladonia* subass. with a dense to closed bed of *Cladonia* spp. In some stands *Cladonia arbuscula* et *mitis* is predominant (see Böcher 1941 b Table 2). On the Swedish west coast *C. impexa* is striking. Sometimes *C. cornuta* et *gracilis* may be frequent. Analyses made by Boerbom (1960 p. 33) show that *C. alcicornis* is common in the Atlantic region. Plant communities analyzed by Sernander (1925 pp. 12-16) and Ardö (1957 pp. 46-47) agree with a *Violo-Corynephoretum*. Sernander (loc.cit.) has reported a *Festuca sabulosa* ass. with scattered *Viola canina* var. *dunensis* and *Hieracium umbellatum* ssp. just inside stands with marram grass. Ardö (loc.cit.) has studied three stands dominated by *Corynephorus canescens* and often with *Festuca arenaria* and *Artemisia campestris* of high frequency, as also can be seen in the typical subassociation of this work. The dominants in the bottom layer are *Cladonia* spp. in the first, *Ceratodon purpureus* in the second and *Rhacomitrium canescens* in the third type. The vegetation of the denuded parts, *Corynephorus canescens* and pioneer mosses, in the outer dunes is regarded a fragment of *Violo-Corynephoretum* (cf. Westhoff & Den Held loc.cit.) instead of a *Corynephoretum maritimum* (see Tüxen 1967 p. 261). Some of the *Corynephorus canescens* soc. on the outer dunes at Sandhammaren are possibly parts of *Cladonio-Corynephoretum* of the inner dune landscape.

Development: *Violo-Corynephoretum* occurs on dry, warm, rather instable, sandy soil habitats on

moderately calcareous or noncalcareous coastal dunes, rarely secondarily on inner dunes. The plant community can be permanent for several years, in a cyclic state between pioneer and lichen phases controlled by aeolian erosion (see Westhoff loc.cit.) often on back dunes. *Violo-Corynephoretum* is developed from *Elymo-Ammophiletum* and is normally in contact with the *Hieracium umbellatum* ssp. subass. The vegetational succession can lead to *Salici-Empetretum* on flat areas. Thus dwarf shrubs on lee slopes are not necessary in a progressive succession. From Denmark Böcher (1941 b, 1954) has reported dune zonations of the xerosere where *Violo-Corynephoretum* is developed into *Salici-Empetretum*. Boerbom (loc.cit.) and van der Maarel & Westhoff (1964) have found a development into a sandy grassland with several plant communities with certain resemblance of the vegetational mosaic at Falsterbo. Very often *Salicetum arenariae* is in contact with *Violo-Corynephoretum*. More seldom, as at Vitemölla, *Antherico-Koelerietum* is bordering.

Ecological remarks: The ecosystem in South Sweden is concentrated in very small parts of the dunes where the environmental factors are somewhat different compared with *Elymo-Ammophiletum*. Important factors are the slow infiltration of precipitation water through the surface soil, the microclimate and the effect of sand accretion. The soil type is a ranker-dune syrosem, in the typical subassociation on certain sites only a syrosem with a minute *A*-layer. In the *Cladonia* subass. the humus zone is about 10 cm. Humus lenses are present. The humus content in the surface soil is about 0.5 % in the typical subassociation and 0.8 % in the *Cladonia* subassociation, in the subsoil probably the same 0.2 %. Corresponding mean values of pH are 5.2 (in KCl 4.1) and 4.9 (3.9) in the surface soil, 5.8 (4.8) in the subsoil respectively. Thus the enlargement of lichens has led to an increase of organic matter and a decrease of soil reaction. Westhoff (loc.cit.) has given a humus content 1-4 % and a pH amplitude 4.4-5.8. The average grain size is about 80 % > 0.2 mm.

Distribution: *Violo-Corynephoretum* is best developed along the north Atlantic coast from the Netherlands to Denmark and to a lesser degree in South Sweden (Erikson 1896, Warming 1909, Sernander loc.cit., van Dieren 1934, Iversen loc.cit., Böcher 1941 b, 1952 a, 1954, 1969, Westhoff loc.cit., Ardö loc.cit., Boerbom loc.cit., van der

Maarel & Westhoff op.cit., Heykena 1965, Westhoff & Den Held op.cit., Ljungberg & Persson, Y. 1973, Runge 1973). Two vicariants, *Helichryso-Jasionetum* in the SW Baltic parts (Libbert 1940, Raabe 1950, Fröde 1957-58, Fukarek 1961, Wojterski 1964 a, Piotrowska & Celiński 1965, Piotrowska 1966) and *Helichryso-Artemisietum balticum* in the SE Baltic parts (Preuss 1911-12, Steffen 1931, Hueck 1932, Paul 1953), occur in the southern Baltic districts. Plant communities described from the island of Gotska Sandön and the southernmost Finnish coast (Lemberg 1933 p. 68, Arwidsson 1938, Pettersson 1965) could be northern fragments of a *Violo-Corynephoretum*. In certain cases *Tortulo-Phleetum arenarii*, *Festuco-Galietum maritimi* and other plant communities of *Galio-Koelerion* can be regarded vicariants of *Violo-Corynephoretum*, especially along the South Atlantic coast and round the British Isles (Tüxen 1937 p. 57, 1967 c, Lebrun et al. 1949 pp. 150-152, Salisbury 1952, Tansley 1953, Vanden Berghen 1958, Klement 1953, Willis et al. 1959, Wiemann & Domke 1967, Westhoff & Den Held 1969) but also on the west coast of Jutland, the province of Bohuslän in W Sweden and southernmost Norway (Böcher 1954, Heykena op.cit., Tüxen 1967 a, Hallberg 1971). *Teesdalia-Corynephoretum* is an inland vicariant of *Violo-Corynephoretum*. In South Sweden the association is distributed along the coast, except at Ängelholm, at Falsterbo and at Furuboda only the typical subassociation and at Sandhammaren only the *Cladonia* subass.

Sociological relationships: *Violo-Corynephoretum* has been regarded a coastal vicariant (Westhoff loc.cit., Tüxen 1955, 1967 c p. 261, Oberdorfer et al. 1967, Runge op.cit.) of a *Corynephoretum canescens* (Tüxen 1928, 1937) and placed into *Corynephorion canescens*. The researches of Westhoff & Den Held (op.cit.) show a closer relationship to *Galio-Koelerion*. Apart from the typical subass. of the association (Westhoff loc.cit.) Boerbom (loc.cit.) has described a *Koeleria albescens* subass. In the present work a *Cladonia* subass. is distinguished. *Galio-Koelerion* (syn. *Koelerion albescens*) has similarities both to *Corynephoretalia* and to *Festuco-Sedetalia* (see Krausch 1968 a), but *Festuca arenaria* is assigned to the second order. *Helichryso-Jasionetum* (Libbert op.cit.) and *Helichryso-Artemisietum balticum* (Fukarek op.cit.) have by Fukarek (op.cit.) been

regarded vicariants of Festuco- Galietum maritimi (see Raabe op.cit., Westhoff & Den Held op.cit. pp. 156-157, Hallberg 1971) instead of a Violo-Corynephoretum or a Tortulo- Phleetum arenarii (see Lebrun et al. 1949, Westhoff & Den Held op.cit. pp. 155-156, Hallberg op.cit.). Two plant communities in this complex are of special kind, viz., a Gentiano- Pimpinellatum saxifragae (Tüxen 1967 a) from southernmost Norway and a Helichrysetum stoechadis (Vanden Berghen 1958) from the South European Atlantic coast both ranked with Galio-Koelerion. On certain places, as at Falsterbo, plant communities of Galio-Koelerion, Thero-Airion and Sedo-Cerastion (syn. Armerion elongatae, Helichrysson arenarii) may be mixed or in mosaic. In some places along the Baltic coast as at Vitemölla Galio-Koelerion is mixed with Koelerion glaucae (see Serander op.cit., Andersson, O. 1950 a, Tüxen 1951) also belonging to Festuco-Sedetalia. Besides this order the short dry grassland contains also Corynephoretalia and Sedo-Scleranthetalia (see Krausch op.cit., Westhoff & Den Held op.cit.) classified into Sedo-Scleranthetea (see Oberdorfer et al. 1967, Krausch op.cit.) or as in this work to Koelerio-Corynephoretea (see Westhoff & Den Held op.cit.).

Teesdalia-Corynephoretum ass.nov. (Table VI, distribution map 10)

Classification: Agrostis canina ssp. montana,

Teesdalia nudicaulis, Filago minima and Aira praecox are characteristic taxa of Teesdalia-Corynephoretum and Thero-Airion. Cladonia glauca, C. degenerans and C. verticillata are differential taxa of Teesdalia-Corynephoretum. The association is split into two subassociations, a typical one negatively characterized and an Artemisia campestris subass. with Artemisia campestris, Hypnum cupressiforme coll., Achillea millefolium and Luzula campestris. A Senecio vernalis variant with Senecio vernalis and Cerastium semidecandrum is present in the typical subassociation, where Polytrichum piliferum is a dominant except in the variant. In the Artemisia campestris subass. three variants have been distinguished, an Euphorbia cyparissias variant with Galium verum and Euphorbia cyparissias, an Oenothera biennis variant with Anthyllis vulneraria and Oenothera biennis and an Asparagus officinalis variant with Arenaria serpyllifolia, Asparagus officinalis and Convolvulus arvensis. Several taxa, such as Corynephorus canescens, Polytrichum piliferum, Rumex tenuifolius, Scleranthus perennis, Jasione montana, Cladonia furcata, C. rangiformis, Ceratodon purpureus, Helichrysum arenarium, Carex arenaria, Thymus serpyllum, Brachythecium albicans, Rhacomitrium canescens, Trifolium arvense, T. campestre, Cornicularia aculeata, Hypericum perforatum, Dianthus deltoides, Campanula rotundifolia, Ononis repens, Herniaria glabra, Potentilla argentea,



Fig. 8. Teesdalia-Corynephoretum Artemisia campestris subass., on impure glacifluvial sand. Ålstorp 1973. Photo B. Wallén.

Vicia lathyroides and *Armeria maritima* var. *elongata*, are of high order and ranked with *Festuco-Sedetalia* and *Koelerio-Corynephoretea*. Some companion taxa belong to *Vaccinio-Piceetea* such as *Cladonia arbuscula et mitis* (only *arbuscula*), *C. cornuta et gracilis*, *C. impexa*, *Cetraria islandica* and *Pinus sylvestris* juv. Other companion taxa are *Agrostis tenuis* and *Hieracium pilosella*, often dominants, *Hypochoeris radicata*, *Hieracium umbellatum*, *Cladonia* spp. and several bryophytes.

Structure: The vegetation consists of a double-layered, open to dense, grassy plant community composed of many hemi-cryptophytes and therophytes. The physiognomy is determined by *Corynephorus canescens*, as a pioneer very typical in tufts on the bare sandy grassland, sand pits or arable land. The tufts are intensively green, with a tint of blue and red, both low-growing and spread in a circle or robust and upright. In the interspaces *Senecio vernalis* may be found. Somewhere *Polytrichum piliferum* totally covers the ground, more seldom together with *Rhacomitrium canescens*. In the typical subassociation the number of species are smaller compared with the *Artemisia campestris* subass., probably an effect of the very closed moss layer. In the second subassociation the dominants may vary from stand to stand, as *Hieracium pilosella* and *Artemisia campestris*. In certain closed stands the debility of *Corynephorus canescens* is obvious. Instead *Carex arenaria* and *Thymus serpyllum* are striking. On some places *Trifolium arvense* is prominent. The bottom layer of the *Artemisia campestris* subass. consists of different cryptogams. *Ceratodon purpureus* and *Cladonia glauca*, may be more abundant than *Polytrichum piliferum*. On dry fallows *Rumex tenuifolius* is important, red in colour on a weakly developed moss layer, in some places related to an *Armeria elongata* - *Rumex tenuifolius* ass. (see Tüxen 1951 Table 4). The structural changes between *Corynephorus canescens*, *Agrostis canina* ssp. *montana* and *A. tenuis* are characteristic of the glaci-fluvial sandy grassland. The plants are both regularly dispersed and clustered (see Mattiasson 1971). On different sandy hills *Aira praecox* and *Filago minima* may be frequent. From East Scania Andersson, O. (1950) and Mattiasson (op.cit.) have described a *Cladonia*-rich community, often on sandy slopes and similar to a *Cladonia* subass. (see Hohenester 1960 p. 44) or a *Cladonia* variant (see Krausch 1968 a Table 1).

Development: *Teesdalia-Corynephoretum* occurs chiefly on dry glaci-fluvial sand with weak tendency to podsolation and often in mosaic with *Agrostio-Callunetum*. *Teesdalia-Corynephoretum* can be developed into other Thero-Airion communities probably into *Festuco-Thymetum serpylli* (see Juraszek 1928 p. 592, Tüxen 1937, Westhoff & Den Held 1969) and *Agrostietum tenuis* (Arndt 1956, Ljungberg & Persson, Y. 1973), both rather fragmentary in Sweden. The result is a closing of the plant cover as in the *Armeria elongata* - *Rumex tenuifolius* ass. (Tüxen 1951 Table 5 B) or the *Medicago falcata* comm. (Mattiasson op.cit. Table 5) with an *Agrostis tenuis* var., regarded as a poor meadow on dry soils. *Teesdalia-Corynephoretum* can also border on another type of poor meadow, the *Festuca ovina* - *Rumex acetosa* comm., especially on verges and headlands. Edges of arable land and young fallows are often dominated by *Agrostis tenuis*. The closed *Teesdalia-Corynephoretum* seems to correspond to a *Spargulo-Corynephoretum Festuca ovina* subass. proposed by Krausch (1968 Table 1), rich in plants from *Festuco-Sedetalia* such as *Helichrysum arenarium*, *Thymus serpyllum* and *Jasione montana*. On calcareous soils in East Scania *Teesdalia-Corynephoretum Artemisia campestris* subass. is normally in contact with *Koelerion glaucae* replacing Thero-Airion or *Armerion elongatae*, which on the Continent seems to be the rule according to Krausch (op.cit. p. 79). The variant with the heliophytes *Galium verum* and *Euphorbia cyparissias* on dry sun-exposed places may be a transitional stage between Thero-Airion and *Sedo-Cerastion* (see Westhoff & Den Held op.cit.). Certain pioneer communities seem to precede *Teesdalia-Corynephoretum*. An *Arnoseretum minimae* (see Klemm 1970 p. 14) is lacking or nearly absent. It occurs on poor rye fallows, often with companion taxa from *Koelerio-Corynephoretea*. Instead a *Holcus mollis* - *Senecio vernalis* comm. has increased its range and is rapidly colonizing restored sand pits. Although *Teesdalia-Corynephoretum* is of anthropogenous origin and appears in a vegetational mosaic, a succession to *Agrostio-Callunetum* and further to an oak forest is obvious.

Ecological remarks: The ecosystem forms a short sandy grassland on a poorly drainable soil. The soil type is a ranker or a podsol-ranker, often with the stratification destroyed as a result of the human influence. The surface soil consists of a dark humus

concentrated with small roots, A-horizon (<20 cm). This zone is transformed into a yellowish mineral soil in some places with rusty mottling (see Table XXII). Thus B- and C-horizons could be included. As Juraszek (op.cit. p. 593) has shown, a transitional zone (A-B) could be present below the A-layer. In the typical subassociation the humus content is about 2 % in the surface soil and 0.7 % in the subsoil. A very small increase in the *Artemisia campestris* subass. has been found, 2 % and 0.9 % respectively. Compared with *Cladonio-Corynephorum* and *Violo-Corynephorum* these figures are high. The mean values of pH are 4.6 (in KCl 4.0) in the surface soil and 4.9 (4.5) in the subsoil in the typical subassociation. Corresponding figures for the *Artemisia campestris* subass. are 5.3 (4.3) and 5.8 (4.5) respectively, which is a small decrease of the soil reaction. Compared with *Cladonio-Corynephorum* and *Violo-Corynephorum* the soil reaction of *Teesdalia-Corynephorum* is nearly the same. Volk (1931 Table 10) has given a pH-amplitude of 4.7-5.8. From East Scania Mattiasson (op.cit.) has reported 4.4-5.9. Marshall (1967 p. 210) has noticed a wider amplitude in the whole area of *Corynephorus canescens* in Europe. The main grain size consists of fine and medium coarse sand, about 65 % > 0.2 mm, which is an increase of the smaller fractions compared with *Cladonio-Corynephorum* and *Violo-Corynephorum*.

Distribution: *Teesdalia-Corynephorum* is regarded a northern vicariant, in the Baltic area (Erikson 1896, Libbert 1932-33 Table 21, Böcher 1941 a Table 16:1-5, Waldheim 1947 pp. 54-55, Andersson, O. op.cit., Weimarck 1950 p. 140, Tüxen 1951 Table 5, Passarge 1960 Table 1, 1964 Table 79, Piotrowska & Celiński 1965 Table 10, Piotrowska 1966, Mattiasson 1970, 1971, Klemm op.cit. Table 33 *Agrostis tenuis* var., Larsson, A. 1971), of the sub-Atlantic *Ornithopodo-Corynephorum* (Volk 1931, Tüxen 1937, Lebrun et al. 1949 p. 149, Oberdorfer 1957 p. 253, Hohenester 1960 Table 1, 1967, Passarge 1960, 1964, Krausch 1968 Table 1, Westhoff & Den Held op.cit.) and the sub-Continental *Veronico-Corynephorum* (Juraszek op.cit., Kobendza 1930, Steffen 1931 Table 44, Klika 1934, Kornas 1957, Oberdorfer 1957 p. 248, Fröde 1957-58 pp. 296-297, Passarge 1960, 1964, Rychnovská-Soudková 1961 Beilage Fig. III a). In South Sweden the plant community is mainly found on inland glaciifluvial sands. Of a special kind is an

Ornithopus perpusillus - *Festuca trachyphylla* soc. (Suneson 1942) from the province of Blekinge and very unique in Sweden. Related coastal Thero-Airion communities are brought together under the following vegetation unit, the *Pleurozium schreberi* - *Agrostis tenuis* comm.

Sociological relationships: In earlier works (Steffen op.cit., Volk op.cit., Libbert op.cit., Tüxen 1937) the *Corynephorus* vegetation was often included in one complex, often called *Corynephorum* with plants both from *Corynephoralia* and *Festuco-Sedetalia*, separated into initial, optimal and degenerated stages or typical subassociation, *Agrostis canina* subass. and *Cladonia* subass. (Tüxen op.cit.). Passarge (1960, 1964) separated the two vicariants *Ornithopodo-Corynephorum* and *Veronico-Corynephorum* ranked with a *Filagini-Corynephorion* from *Spergulo-Corynephorum* associated with a *Spergulo-Corynephorion*. The present *Teesdalia-Corynephorum* split into a typical subassociation and an *Artemisia campestris* subass., as well as the vicariants *Ornithopodo-Corynephorum* and *Veronico-Corynephorum* belong according to Westhoff & Den Held (op.cit.) to a Thero-Airion. Passarge (1964 p. 241) has pointed out a *Teesdalia nudicaulis* race in a closed South Baltic area, in the present work transformed into a *Teesdalia-Corynephorum*, valid for the investigation area. Very similar to a *Teesdalia-Corynephorum* is an *Aira praecox* - *Sedum rupestre* -ass. (Tüxen 1951). Passarge (1960, 1964) placed *Filagini-Corynephorion* into *Corynephoralia*. Westhoff & Den Held (op.cit.) arranged Thero-Airion, included into *Corynephorion* according to Klika (1931) and Krausch (1968), into *Festuco-Sedetalia* of *Koelerio-Corynephorum*, according to Oberdorfer et al. (1967) to Thero-Airetalia prov. of *Sedo-Scleranthetea*.

Pleurozium schreberi - *Agrostis tenuis* community comm. nov. (Table VII, distribution map 11)

Classification: *Agrostis tenuis* and *Pleurozium schreberi* form a local differential combination. *Amphiphila arenaria* and *Deschampsia flexuosa* are differential taxa of a *Deschampsia flexuosa* variant. *Carex arenaria* constitutes a second variant. Besides *Carex arenaria* also *Cornicularia aculeata*, *Cladonia furcata*, *Corynephorus canescens*, *Ceratodon purpureus*, *Festuca arenaria*, *Viola tricolor* ssp. *curtisii*, *Aira praecox* and *Polytrichum piliferum* are of high

order, belonging to Festuco-Sedetalia and Koelerio-Corynephoretea. *Galium verum* and *Polypodium vulgare* are among the companion taxa as well as *Cladonia* spp., *Parmelia physodes*, *Dicranum scoparium* and *Polytrichum juniperinum*.

Structure: The vegetation consists of a dense to closed, double-layered plant community rich in hemicryptophyte graminids. The physiognomy is determined by *Deschampsia flexuosa* (see Böcher 1941 a Table 12) or *Carex arenaria* in separated stands or both in the same stand. *Pleurozium schreberi* is a dominant in the bottom layer. *Ammophila arenaria* is in some places a common relict from Elymo-Ammophiletum.

Development: The plant community occurs on fixed dunes without sand accretion on acid mineral soils, as a rule in contact with Elymo-Ammophiletum, Cladonio-Corynephoretum or Salici-Empetretum, in some places also with an anthropogenous vegetation. Fukarek (1961 Table 14) has separated a *Helichryso-Jasionetum Agrostis tenuis* subass. developed in several ways, also from lichen-rich stands. The present plant community is developed normally from a degenerated Elymo-Ammophiletum and more rarely from a Cladonio-Corynephoretum.

Ecological remarks: The soil type is regarded a ranker with small roots concentrated in the humus layer in the surface on the brownish mineral soil. The humus content in the surface soil is 2.7 %. The soil reaction is very acid. The pH at 0-5 cm is 3.9 (in KCl 3.5), lower than surrounding contact vegetation.

Distribution: Within the investigation area the *Pleurozium schreberi* - *Agrostis tenuis* comm. has been found at Ängelholm. The analyses made by Larsson, A. (1971 Table 9) show a related plant community in the Vomb area. In the province of Blekinge Berglund (1963 Table 3) has reported a similar grassland vegetation. In a transection from Jutland to the Baltic States from different places other Thero-Airion plant communities are found (see Iversen 1936 Table 52, Böcher 1941 a, 1945, Fukarek loc.cit., Steffen 1931, p. 272) of certain relationships.

Sociological relationships: The plant community seems to vary from a Festuco- Galietum maritimi along the North Atlantic and SW Baltic coasts (see Tüxen 1937, Westhoff 1947, Boerbom 1960, Westhoff & Den Held 1969, Hallberg 1971) belonging to Galio-Koelerion and is more closely affiliated

with Thero-Airion. A *Carex arenaria* - *Jasione montana* comm. from East Scania (Andersson, E. & Nilsson, J. 1971) represents a transitional stage. An *Agrostietum tenuis* (Arndt 1956, Ljungberg & Persson, Y. 1973) as well as certain closed *Carex arenaria* communities in the inland are typical of Thero-Airion. Fukarek (op.cit. p. 120) has described a '*Deschampsia flexuosa*-Rasen', aside from an *Agrostis tenuis* subass. of *Helichryso-Jasionetum*, also with poor meadow plants and of some interest in this Thero-Airion complex.

Antherico- Koelerietum glaucae (Erikson 1896) Andersson 1950 (sub nom. *Koelerietum glaucae*) (Table VII, distribution map 12)

Classification: *Koeleria glauca*, *Festuca polesica*, *Dianthus arenarius*, *Astragalus arenarius* and *Androsace septentrionalis* are characteristic taxa of *Antherico- Koelerietum glaucae* and *Koelerion glaucae*. *Cladonia arbuscula et mitis* and *C. chlorophaea* coll. are among a *Cladonia* subass. *Anthericum liliago* and *Cerastium semidecandrum* coll. belong to an *Anthericum liliago* variant. Several taxa are ranked with Festuco-Sedetalia and Koelerio-Corynephoretea such as *Carex arenaria*, *Cornicularia aculeata*, *Cladonia furcata*, *C. pityrea*, *C. alpicornis* var., *Corynephorus canescens*, *Ceratodon purpureus*, *Thymus serpyllum*, *Rhacomitrium canescens*, *Sedum acre*, *Hypnum cupressiforme* var. *lacunosum*, *Helichrysum arenarium*, *Hieracium umbellatum* ssp. *Viola rupestris*, *Jasione montana* var. *littoralis*, *Phleum arenarium*, *Anthyllis vulneraria* ssp. *maritima* and *Tortula ruralis* var. *ruraliformis*. A group of thermophytes, *Galium verum*, *Anemone pratensis*, *Artemisia campestris* and *Pimpinella saxifraga*, are associated with the companion taxa as well as certain trivial cryptogams.

Structure: The vegetation consists of an open to closed plant community. The double-layered stands are normally very rich in xerophytes with a dense mat of mosses and lichens. In a typical moss rich subassociation of *Antherico- Koelerietum glaucae* (see Andersson, O. & Waldheim 1946, Andersson, O. 1950 a, Tüxen 1951, Mattiasson 1970, 1971) the vegetation often grows in small segments with short grasses, rosette plants, cushion species, ligneous herbs such as *Thymus serpyllum* and *Artemisia campestris* and succulents such as *Sedum acre*. The



Fig. 9. *Antherico- Koelerietum glaucae*, on a calcareous glacifluvial slope. Vitemölla 1946. Photo O. Andersson, Skånes Naturskyddsför. Arkiv.

hemicryptophytes are reduced in number and the geophytes are absent. Instead different therophytes, including both winter and summer annuals, have fine growing possibilities. Though rich in plants the vegetation may be monotonous and poor compared with the Continental steppes. *Androsace septentrionalis* and *Anthericum liliago* have their flower maximum in late spring, *Dianthus arenarius*, *Helichrysum arenarium* and *Thymus serpyllum* in summer. The white colour of the flowers in spring is followed by a spectrum of white, yellow, red and blue during the rest of the vegetation period. In winter the plant cover is green or grey. *Antherico-Koelerietum glaucae* can in places contain sub-Atlantic elements as *Carex arenaria*, *Phleum arenarium* and *Silene conica* (see Krausch 1968 p. 93). The most prominent mosses are *Rhacomitrium canescens* especially on poor stands (Andersson, O. & Waldheim op.cit. Table 5), *Tortula ruralis* var. *ruraliformis* in rich habitats and very rarely *Tortella inclinata* in an extraordinary environment (Andersson, O. & Waldheim loc.cit.).

In the *Cladonia* subass. (see Sterner 1922 Table 3, Mattiasson 1971) the number of plants has been reduced and the vegetation is more open and dominated by the short grasses *Koeleria glauca*, *Corynephorus canescens* and *Festuca polesica*.

Phleum arenarium seems to thrive scattered in both the typical subassociation and the *Cladonia* subass. Mattiasson (op.cit.) has noticed the occurrence of *Bromus hordeaceus* ssp. *Thominii*, an effect of the grazing, more linked to the latter subassociation. *Anthericum liliago* and probably also *A. ramosum* (Sterner loc.cit.) may be frequent in the lichen stands. The bottom layer is dominated by *Cladonia arbuscula* et *mitis* accompanied by *C. furcata* and *Cornicularia aculeata*. The lichen structure is not constant but differs on several places. *C. rangiformis* and *C. alcornis* var. are often more frequent (see Sterner loc.cit., Tüxen loc.cit., Mattiasson 1971). *Cetraria nivalis* may also be very striking (Mattiasson op.cit.) together with *Hypnum cupressiforme* var. *lacunosum*.

Development: *Antherico- Koelerietum glaucae* occurs on dry, sandy calcareous soils, especially on glacifluvial plains or slopes. In some places the plant community may possibly be regarded as a substitute of thermophilic thin pine forests as on the opposite Baltic coast. Mattiasson (op.cit.) has described the vegetational succession from *Antherico-Koelerietum glaucae* via *Teesdalio-Corynephoretum* to an *Agrostio-Callunetum* and further to a woodland rather similar to a xerothermic development of the vegetation on the Continent (see Klika 1931, 1934).

Besides the contacts to Teesdalio-Corynephorum the plant community appears in the vicinity of dry meadows (see Sterner op.cit. Table 1, Andersson, O. & Waldheim op.cit., Andersson, O. op.cit., Mattiasson op.cit.). According to Andersson, O. (op.cit. p. 159) the vegetation is seldom entirely continuous but interrupted by sandy patches, mainly the result of animal activity and necessary to retain the character of Antherico-Koelerietum. If the interference is stopped some lime-favoured therophytes and mosses disappear and *Rhacomitrium canescens* closes the bottom layer leading to a small leaching in the surface soil.

Ecological remarks: The ecosystem is confined to a sandy substratum with a high content of lime, 5-20 % (Andersson, O. loc.cit.). The soil profile shows a pararendzina, on sites with less calcareous soils probably also a paranker (see Schroeder 1972 p. 102). Waldheim (1947 p. 77) has discussed steppe soils of rendzina type. Schlichting (1954 p. 48) has mentioned a dry mull pararendzina (cf. Pålsson 1974 Fig. 7) and ranker. The A-horizon with grey-brownish humus varying between 10-25 cm in thickness (Andersson, O. loc.cit., Linnermark 1966 Fig. 13) is situated on the unaltered mineral horizon. On degenerated stands with *Rhacomitrium canescens* a tendency to podsolation may be seen. In surface soil at Vitemölla the pH is 8.4 (in KCl 7.6) and at 40-50 cm 9.2 (8.5). Andersson, O. & Waldheim (op.cit. p. 114) have given a mean value of pH 7.7. Not only the alkaline soil reaction is of importance for maintaining the plant community but also the climate. Cold winters and many frost days can damage the sub-Atlantic elements, such as *Corynephorus canescens*. The Continental *Koeleria glauca* can grow throughout the year.

Distribution: *Koelerion glaucae*, containing many Continental plants (see Sterner op.cit.) with northern outposts in the Baltic area and in Denmark (Raunkiaer 1914, Böcher 1945), has the main area of distribution in East-Central Europe (Klika 1931, 1934) and with certain western outposts (Volk 1931, Oberdorfer 1957). In Poland and DDR there is a Festuco- *Koelerietum glaucae* (Kobendza 1930 Table 7, Libbert 1932-33, Kornas 1957, Passarge 1964, Berger-Landefeldt & Sukopp 1965, Piotrowska & Celiński 1965, Piotrowska 1966, Krausch 1968). Antherico- *Koelerietum glaucae* (Erikson 1896, Sernander 1919, Andersson, O. &

Waldheim op.cit., Andersson, O. op.cit., Weimarck 1950, Tüxen op.cit., Mattiasson 1971, Pålsson op.cit.) is sparsely found in South Sweden and regarded different from the *Festuca polesica* vegetation round the SE Baltic coasts (Sernander 1925, Regel 1928, 1944, Lippmaa 1931 p. 59, Steffen 1931 p. 283, Andersson, O. & Waldheim op.cit., Andersson, O. op.cit., Tüxen 1951, Paul 1953 Table 19, Bergholz & Holmquist 1955). Certain marginal plant communities in the north, possibly outside of the *Koelerion glaucae* area may be mentioned: *Thymus serpyllum* - *Galium verum* comm. from Estonia (Pastak 1936-37), *Festuca polesica* dunes from South Finland (Lemberg 1933 pp. 57-60) and an inland, dry grassland with *Gypsophila fastigiata* (Samuelsson 1910, Jalas 1950) from Middle Sweden and Finland.

Sociological relationships: Compared with a Festucetum *polesicae* (Regel 1928) Antherico-Koelerietum *glaucae* is very different in physiognomy and floristical composition. The *Festuca polesica* dunes (Lemberg op.cit.) and the *Festuca sabulosa* - *Rhacomitrium* ass. (Sernander 1925 Table 2) as well as the analyses made by Steffen (loc.cit.) and Paul (loc.cit.) show that a division of the Koelerietum (Andersson, O. op.cit.) or *Festuca polesica* - *Dianthus arenarius* ass. (Tüxen 1951), into an exclusive Antherico- *Koelerietum glaucae* rich in steppe plants and a *Thymus serpyllum* - *Festuca polesica* ass. (see Regel 1944) on dunes and sandy plains is correct. The latter association seems to overlap in some places with a *Violo-Corynephorum* along the Baltic coasts; thus compared with an earlier work (Olsson 1971) a small revision is now made. The division of Antherico-Koelerietum into a typical subassociation, moss rich, and a *Cladonia* subass. agrees with the results of Mattiasson (1971). The sub-Continental-Continental *Koelerion glaucae* (see Volk op.cit., Klika 1934) is to the west replaced by an *Armerion elongatae* (Krausch 1968 a). *Helichrysion arenariae* (Tüxen 1951) is a transitional stage. Krausch (op.cit.) has given four associations, Linario- *Koelerietum glaucae*, Festuco- *Koelerietum glaucae*, *Dianthus arenariae* - Festucetum *caesia* and Jurineo- *Koelerietum glaucae*, belonging to *Koelerion glaucae*, together with an *Armerion elongatae* placed into Festuco-Sedetalia (see also Oberdorfer et al. 1967 p. 34).

Poor meadow vegetation

Festuca ovina - *Rumex acetosa* community comm.nov. (Table VI, distribution map 13)

Classification: *Rumex acetosa*, *Holcus lanatus*, and *Plantago lanceolata* are local characteristic taxa of a *Festuca ovina* - *Rumex acetosa* comm. *Festuca ovina*, *Pleurozium schreberi*, *Anthoxanthum odoratum*, *Hylocomium splendens* and *Stellaria graminea* are differential taxa towards *Teesdalia-Corynephorum*. *Knautia arvensis*, *Arrhenatherum elatius*, *Veronica chamaedrys* and *Rhytiadelphus squarrosus* are ranked with *Molinio-Arrhenatheretea*. *Agrostis tenuis*, *Hieracium pilosella* and *Festuca rubra* together with *Artemisia campestris*, *Achillea millefolium* and *Luzula campestris* also common to an *Artemisia campestris* subass. of *Teesdalia-Corynephorum* are the most prominent companion taxa. Also a group of plants from *Koelerio-Corynephoretea* are normally present.

Structure: The vegetation consists of a closed double-layered plant community dominated by *Hieracium pilosella* and *Festuca ovina*. Other herbs and graminids are scattered. The bottom layer is composed of several mosses as *Pleurozium schreberi*. The structure is related to a 'Festuca ovina-backäng' from the province of Uppland (Almquist 1929 Table 46).

Development: The plant community occurs on the sandy grassland or pastures, often in contact with *Agrostio-Callunetum* or *Agrostio-Quercetum roboris*, in some places also a component of the verges.

Ecological remarks: The ecosystem is regarded a very poor meadow linked to the heaths. Compared with other vegetation of *Molinio-Arrhenatheretea* the present plant community seems to be uninfluenced by the ground water (see Klemm 1970 p. 5).

Distribution: The *Festuca ovina* - *Rumex acetosa* comm. is possibly a transitional stage between the 'Festuca ovina -backäng' of the oak region (Almquist op.cit. p. 215) further to the north and the southern Continental *Festucetum rubrae* (Steffen 1931 p. 234, Böcher 1945 Table III, Oberdorfer 1957 p. 225, Passarge 1964, Jessen 1968 Table 23, Klemm loc.cit.). In the province of Blekinge a well-developed *Festuca ovina* - *Rumex acetosa* comm., according to Berglund (1963 Table 3) an *Ononis repens* - *Cirsium acaule* comm., is present.

Sociological relationships: Oberdorfer (1957) has

described a *Trifolio-Festucetum rubrae*, according to Passarge (1964) *Festucetum rubrae*, of *Arrhenatherion elatioris*. Probably the *Festuca ovina* - *Rumex acetosa* comm. also belongs to this alliance ranked with *Arrhenatheretalia* of *Molinio-Arrhenatheretea* (Tüxen 1937).

Dwarf shrub and bush vegetation

Dwarf shrub vegetation

Salicetum arenariae (Warming 1909 em. Regel 1928) ass.nov. (Table VIII, distribution map 14)

Classification: *Salix arenaria* is a characteristic dominant of *Salicetum arenariae*. *Ammophila arenaria* and *Festuca arenaria* are differential taxa of an *Ammophila arenaria* subass. *Carex acuta*, *C. nigra*, *Galium uliginosum* and *Veronica scutellata* are among a *Carex nigra* subass. *Corynephorus canescens*, *Jasione montana*, *Elymus arenarius*, *Parmelia physodes* and *Viola tricolor* ssp. *curtisii* belong to a *Corynephorus canescens* variant of the *Ammophila arenaria* subass. *Calluna vulgaris*, *Luzula multiflora* and *Empetrum nigrum* are ranked with *Nardo-Callunetea*. Companion taxa from *Koelerio-Corynephoretea*, e.g., *Ceratodon purpureus* and *Carex arenaria* and from *Molinio-Arrhenatheretea* are present, further more *Betula pubescens* juv. and *Pinus sylvestris* juv.

Structure: The vegetation consists of a dense to closed, chiefly single-layered plant community. *Salicetum arenariae* is a very specialized association dominated by *Salix arenaria* forming cycles on the dunes (Ranwell 1960 p. 130). Normally plants from *Elymo-Ammophiletum*, *Violo-Corynephorum* and *Salici-Empetretum* grow as relicts in the interspaces between the *Salix arenaria* shrubs. *Jasione montana* var. *littoralis* is striking with its blue flowers. The stands vary in height up to half a metre. Some authors (Nilsson, A. 1905, Warming 1909, Lemberg 1933) have reported small monospecific *Salix arenaria* dunes. Certain degenerated stands with *Parmelia physodes* and bryophytes are probably a transitional stage to a *Salici-Empetretum* (see Runge 1973 pp. 189, 222). In the *Carex nigra* subass. the vegetation is in several cases more sparse, especially on wide, moist, sandy plains (see Nilsson op.cit. Fig.

7, Warming op.cit. Fig. 191) with irregular growth of *Salix arenaria*. The Atlantic dune slacks are often occupied by a *Salicetum arenariae* more homogenous and rich in species (see van Dieren 1934 Tables 38-39, Tansley p. 863, Willis et al. 1959, Ranwell op.cit., van der Maarel & Westhoff 1964).

Development: *Salix arenaria*, dependent on a wet environment for growth and a dry for migration, responds on the sand cover by renewed growth with a continuous root generation. On old acid sand *Salix arenaria* is suppressed. Certain shoots are creeping with a centrifugal growth. On dune horsts isolated clones may be found, about 50 years old (cf. Ranwell loc.cit.). If the sand accretion is stopped and the *Salix arenaria* dunes begin to erode, a degeneration phase of the cycle is started (see Warming op.cit. Fig. 88, Ardö 1957 Fig. 29). Also Paul (1944 pp. 328-337, 1953 pp. 295-296) has pointed out a development from wetter to drier parts in the dune system but the cycle is more complicated with the presence of both *Salix arenaria* and *S. daphnoides*. *Salicetum arenariae* is normally in contact with *Elymo-Ammophiletum*, *Violo-Corynephoretum*, *Salici-Empetretum* and *Molinio-Myricetum gale* *Salix arenaria* subass., but it is not regarded a typical stage in a xerosere, different from a *Polypodio-Salicetum* (Boerbom 1960, Runge 1973), which is a component of the dune succession to tall shrubs of *Hippophae rhamnoides* or further to an oak forest. Libbert (1940 Table 7) has described a degeneration phase of *Helichryso-Jasionetum* with *Salix arenaria*.

Ecological remarks: The ecosystem is limited to habitats with a combination of ground water influence and sand accretion, related to a cyclic subseral succession in a mobile dune slack complex (Ranwell loc.cit.). The soil type is a dune syrosem in the *Ammophila arenaria* subass. and a ranker in the *Carex nigra* subass. (see Ranwell 1959 Fig. 10). In the first one certain root layers and big extending roots occur. In the second one the roots are limited by the fluctuating water table. The mean pH values in the surface soil are 6.0 (in KCl 4.8) in the *Ammophila arenaria* subass. and 5.5 (4.4) in the *Carex nigra* subass. Corresponding figures of the subsoil are 6.3 (4.8) and 5.3 (4.4) respectively. The soil reaction is similar to that of *Elymo-Ammophiletum* but the humus content is somewhat higher, about 0.6 % in the first and 1.9 % in the second subassociation in the surface soil and about 0.2 % in the subsoil. The

grain size can vary, from one stand at Tönnersa about 98 % > 0.2 mm.

Distribution: *Salicetum arenariae* occurs in the northern and north-western parts of Europe, common on the British Isles (Ranwell 1959, 1960, Tansley op.cit., Willis et al. op.cit., Chapman 1964) and along the coasts from the Netherlands to Norway called *Pyrolo-Salicetum*, *Polypodio-Salicetum* or *Salicetum repentis* (Warming op.cit., Raunkiaer 1914, van Dieren op.cit., Iversen 1936 p. 153, Westhoff 1947, Ardö op.cit. p. 48, Boerbom 1960, van der Maarel & Westhoff op.cit., Heykena 1965, Westhoff & Den Held 1969 p. 245, Runge op.cit.). In the Baltic districts with decreased salinity *Salicetum arenariae* can also advance seawards to the beach (Nilsson, A. op.cit., Hesselman 1908, Regel 1928, Tomuschat & Ziegenspeck 1929, Steffen 1931, Lemberg 1933 p. 89, Lippert op.cit., Paul 1944, 1953, Andersson, O. 1950 p. 153). Within the investigation area *Salicetum arenariae* occurs along the coast from Haverdal to Ängelholm, at Sandhammaren and Furuboda. At Tönnersa and Sandhammaren there are also a *Carex nigra* subass.

Sociological relationships: Warming (op.cit. p. 135) has proposed a *Salix arenaria* comm. changed to a *Salicetum repentis argenteae* by Regel (op.cit.). The arrangement of this association into a phytosociological system is incomplete. Tüxen (1952, 1955) has placed a *Polypodio-Salicetum* (see Boerbom op.cit.) into *Salicion arenariae*, according to Westhoff & Den Held (op.cit.) doubtful as a separate alliance, belonging to the termophilic *Prunetalia spinosae* including the tall shrubs of *Hippophae rhamnoides*. Doing (1962, 1963) has preferred to combine the short-growing *Salix arenaria* stands with the boreo-Atlantic *Vaccinio-Genistetalia* and introduced *Empetro-Salicion arenariae* of a *Genisto-Callunetalia*, belonging to *Nardo-Callunetea* (Doing 1962 p. 41, 1963 p. 54). It seems difficult to make a conjunction between *Salicion arenariae* and *Empetrium nigri* (Böcher 1943, Schubert 1960) forming an *Empetro-Salicion arenariae*. The first alliance has a wider range than the second one. Also the cyclic qualities are different between a *Salicetum arenariae* of the first and *Salici-Empetretum* of the second alliance. Thus in South Sweden and further to the north it is more adequate to place *Salicion arenariae* together with other dwarf shrubs into *Vaccinio-Genistetalia* (Schubert op.cit.) of *Nardo-Callunetea*.

Salici-Empetretum R.Tx. (1937) 1955 (Table IX, distribution map 15)

Classification: *Empetrum nigrum* is a characteristic taxon of *Salici-Empetretum* and *Empetrium nigri*, also forming an *Empetrum nigrum* soc. *Festuca arenaria*, *Viola canina* var. *dunensis* and *Artemisia campestris* are differential taxa of a *Festuca arenaria* subass. *Polypodium vulgare*, *Ammophila x baltica*, *Polytrichum juniperinum* and *Hypochoeris radicata* are differential taxa of a *Polypodium vulgare* subass. *Lophocolea heterophylla*, *Lotus corniculatus*, *Pinus sylvestris* juv. and *Erica tetralix* are differential taxa of a *Lophocolea heterophylla* subass. A specific group of cryptogams, *Dicranum scoparium*, *D. undulatum*, *Pleurozium schreberi*, *Cladonia arbuscula* et *mitis*, *C. chlorophaea* coll. and *C. impexa*, from the two latter subassociations, are common to a *Calluna vulgaris* soc. of a *Cladonio-Callunetum* belonging to *Cladonio-Callunion* prov. The plant group is also a differential taxa combination of the *Festuca arenaria* subass. *Calluna vulgaris*, *Hypnum ericetorum*, *Salix arenaria*, *Luzula campestris*, *L. multiflora*, *Lycopodium clavatum*, *Arctostaphylos uva-ursi* and *Hypochoeris maculata* are of high order and ranked with *Vaccinio-Genistetalia* and *Nardo-Callunetea*. The companion taxa among *Koelerio-Corynephoretea* are such as *Carex arenaria*, *Cornicularia aculeata* and *Corynephorus canescens*, among *Vaccinio-Piceetea* e.g., *Cladonia cornuta* et *gracilis* and *C. rangiferina*, *Deschampsio-Quercetea robori* -*petraeae* and *Molinio-Arrhenatheretea*. Of other companion taxa may be mentioned: *Parmelia physodes*, *Pohlia nutans*, *Cephaloziella* sp., *Ammophila arenaria*, *Brachythecium rutabulum*, *Cetraria glauca*.

Structure: The vegetation consists of a dense to closed single or double-layered plant community dominated by nano-chamaephytes and several cryptogams, especially lichens in the interspaces. *Empetrum nigrum* soc. and *Festuca arenaria* subass. are composed of a low-growing green carpet influenced by a small continuous sand accretion. Heyken (1965 pp. 44-45) has shown some ecomorphological qualities of *Empetrum nigrum*, rosettes and etage growth. In certain stands, principally on back dunes, *Salix arenaria* and *Empetrum nigrum* may be mixed rather homogenously (see Raunkiaer 1914 Table 10:2, Böcher 1943 Table 8:14). *Festuca arenaria* is a third important component. The absence of cryptogams, only scattered *Cornicularia aculeata* and *Polytrichum piliferum*, is according to Böcher (op.cit. p. 44) an effect of the sand accretion in the area of western Sweden and Denmark on the coastal *Empetrum* heaths, often with relicts from *Violo-Corynephoretum*.

In the *Polypodium vulgare* subass. the dominance of *Empetrum nigrum* is reduced in certain stands, although the combination of *Empetrum nigrum* and *Polypodium vulgare* may be constant and dominate or separately marked as a *Polypodioto-Empetretum* (see Westhoff 1947 p. 93) but without characteristic musci. A related floristic structure has been described by Böcher (1954 Table 4:IX) and Runge (1973 p. 189) but lacking *Calluna vulgaris*, to a variant in Westhoff (loc.cit.) physiognomically important in some stands of the *Polypodium vulgare* subass., as at Sandhammaren. In one stand *Betula verrucosa* juv. and *Salix arenaria* are prominent but different in structure compared with a *Polypodio-Salicetum* (Boerbom 1960). In this subassociation

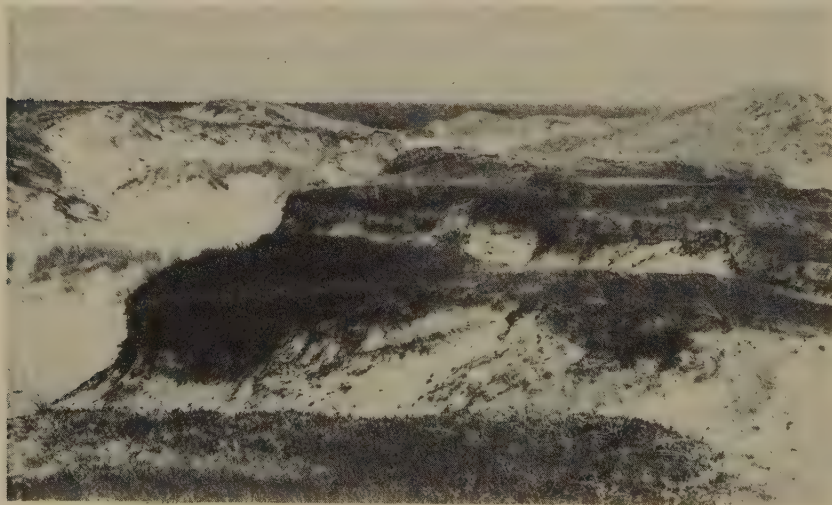


Fig. 10. *Salici-Empetretum Festuca arenaria* subass. Tönnersa 1973. Photo B. Wallén.

the rather uniform moss layer with *Pleurozium schreberi* and *Dicranum scoparium* is striking. The most important lichen is *Parmelia physodes*, in the *Calluna vulgaris* dominated stands also *Cladonia* spp.

Calluna vulgaris is, in several cases, more abundant than *Empetrum nigrum* in the *Lophocolea heterophylla* subass. In some places *Empetrum nigrum* may be luxuriant, as a secondary dominant, spreading out of dead or degenerated shrubs of *Calluna vulgaris* on dry places. *Cladonia* spp., *Pleurozium schreberi* and *Hypnum ericetorum* constitute a great part of the bottom layer. Both Ardö (1957 p. 49) and Gimingham (1961 Table 6) have given *Pleurozium schreberi* as a dominant, and the lichens in subordination. Böcher (1941 b Table 10) has analyzed stands where *Cladonia* spp. are most striking. Of special interest is *Lotus corniculatus*, of diagnostic value in the Atlantic region, but absent at Sandhammaren; therefore *Lophocolea heterophylla* has been the preferred name of this subassociation. In the tables given by Raunkiaer (op.cit. Table 8), Böcher (op.cit. Table 2:4), van Dieren (1934 Tables 45-48) and Heykena (op.cit. Table VI) *Lotus corniculatus* is an important component in a similar *Salici-Empetretum*. On moist stands *Erica tetralix* is scattered. Compared with *Festuca arenaria* subass. and *Polypodium vulgare* subass., often homogenous and short growing, *Lophocolea heterophylla* subass. is irregular and high-growing.

Development: *Salici-Empetretum* occurs on acid, poor mineral soil, in dry or moist habitats on maritime dunes. *Empetrum nigrum* is a pioneer, in some places forming tussocks and growing in patches, with a primary root and creeping shoots with adventive roots in the humus layer. Tüxen (1967 a p. 271) is of the opinion that the more non-calcareous the dune area the easier it is for *Empetrum nigrum* to immigrate and grow. The *Empetrum* heaths on the Swedish west coast and on Jutland take a position between *Violo-Corynephorum* and *Lophocolea heterophylla* subass. As a rule *Salici-Empetretum* is a seral stage in a succession from *Elymo-Ammophiletum* via *Violo-Corynephorum* up to a coastline forest, somewhere also in direct contact with *Elymo-Ammophiletum*. The development of a moss layer, pronounced at Ängelholm, is favoured by a high humidity. The more arid climate at Sandhammaren is preferred by the lichens. The colonization of *Empetrum nigrum*

goes rapidly and facilitates with soil leaching *Cladonia*-rich stands. After settlement *Salici-Empetretum* is developed into a subclimax heath on protected and not too dry places (Böcher 1952 p. 8), landwards dominated by *Calluna vulgaris*. In the inland of Jutland (Böcher 1943 a p. 88) a reverse development from *Calluna* stands to segments with *Empetrum nigrum* and *Vaccinium vitis-idaea* on extremely dry habitats is encountered. Apart from *Elymo-Ammophiletum* and *Violo-Corynephorum*, earlier stages in the succession, *Salici-Empetretum* is in contact with *Cladonio-Corynephorum*, *Salicetum arenariae*, *Calluna vulgaris* soc., initials of oak and pine forests and on moist ground *Molinio-Myricetum gale Salix arenaria* subass.

Ecological remarks: The ecosystem is bound to rather fixed dunes, resistant to the winds, where the water capacity has been improved and the humus content increased as a consequence of the continuous litter supply. Also the leaching effect is more pronounced. The soil type is a ranker or a ranker-dune syrosem as that of *Empetrum nigrum* soc. and *Festuca arenaria* subass., where the A-C stratification is diffuse and humus content 0.4-0.5 %, and the pH 5.4-5.5 (in KCl 4.1-4.2) is nearly the same in the surface soil compared with the subsoil, as a result of the sand burial. In the *Polypodium vulgare* subass. the humus content has increased in the surface soil, about 1.2 %, but decreased in the subsoil, about 0.2 %. The pH is 4.6 (in KCl 3.5) at 0-10 cm, and higher at 50-60 cm, 5.7 (4.7). Also the soil profile is different, compared with *Festuca arenaria* subass., regular although the raw humus is very thin and the A-layer seems to be below 15 cm. The most pronounced stratification is seen in the *Lophocolea heterophylla* subass. where the raw humus concentrated with roots is about 5 cm and the A-layer is up to 20 cm, lying on the brownish or yellowish mineral soil. The humus content in the surface soil has continued to increase, about 3.2 %, in the subsoil about 0.2 %. The soil reaction is similar to that of *Polypodium vulgare* subass., 4.4 (3.4) and 5.9 (4.6). Westhoff (op.cit. p. 95) has given a pH-amplitude of the A-layer of 4.1-5.0 from a Dutch *Polypodio-Empetretum*, Böcher (1941 a, 1954) about 5.0 from the coastal heaths of Jutland. The grain size is strongly variable, in the first subassociation 40 %, in the second 70 % and in the third 80 % exceeding 0.2 mm.

Distribution: *Salici-Empetretum* occurs in the sub-

Atlantic and sub-Continental parts of Northern Europe coasts (see Schubert 1960 Karte 4) in the Atlantic districts probably a Polypodio-Salicetum vicariant (Warming 1909 pp. 160-168; Raunkiaer loc.cit. Table 8, van Dieren op.cit., Tüxen 1937, 1967 a, Christiansen 1938 p. 109, Böcher 1941 b, 1943 a, 1952 a, 1954, Westhoff op.cit., Ardö 1957, Gimingham loc.cit., Heykena op.cit., Nilsson, N.-G. 1966, Westhoff & Den Held 1969, Runge op.cit.) in the Baltic region a Hieracio-Empetretum (Libbert 1940) synonymous with a Salici-Empetretum (Preuss 1911-12 p. 67, Libbert op.cit. Table 7, Fröde 1957-58 p. 300, Fukarek 1961 p. 121, p. 251, Passarge 1964 a, Wojterski 1964 a Table 37, 1964 b Fig. 3). In the Baltic States and the northern parts of the Baltic Sea Salici-Empetretum is dying away and a transition towards other heaths (Steffen 1931 p. 277, Lemberg 1933 p. 91, Paul 1953 Figs. 26-30) with *Antennaria dioica* and *Juncus balticus* is obvious. In South Sweden *Empetrum nigrum* soc. and *Festuca arenaria* subass. are found at Haverdal and Tönnersa and they are also present on Jutland. *Polypodium vulgare* subass. appears at Ängelholm, Falsterbo, Sandhammaren and as a very small fragment at Furuboda where it is an outpost of the western Polypodio-Empetretum. *Lophocolea heterophylla* subass. occurs between Haverdal and Ängelholm on the west coast and at Sandhammaren and is more affiliated with the Baltic vicariant.

Sociological relationships: The investigated Salici-Empetretum is related to a Calluneto-Genistetum empetretosum (Tüxen 1937) changed into Saliceto repentis-Empetretum (Tüxen 1955), Polypodio-Empetretum (Westhoff 1947) and Hieracio-Empetretum (Libbert op.cit.). The present association forming three subassociations, seems to include a secondary plant community by Passarge (op.cit. p. 285) with various shrubs and the stands containing *Calluna vulgaris* with dune species, according to Gimingham (op.cit. Table 6). Schubert (op.cit. pp. 202-203) has separated two suballiances, one montane-subalpine Vaccinio-Empetrition and one coastal Caricio-Empetrition, more linked to the original Empetrition boreale proposed by Böcher (1943 a) changed to Empetrition nigri (Schubert loc.cit.), belonging to Vaccinio-Genistetalia, including low-growing dwarf shrubs in the sub-Atlantic and sub-Continental area. Empetrition nigri or according to Doing (1962 p. 54) Empetro-Salicion arenariae is in the NE Europe in contact with

Loiseleurio-Vaccinietea (Eggler 1952) with Arctic and Arctic-alpine plants. Preising (1949) combined Calluno-Ulicetalia (Tüxen 1937), synonymous of Vaccinio-Genistetalia and Nardetalia to Nardo-Callunetea occupying acidophilic dwarf shrub heaths in Central and Northern Europe.

Calluna vulgaris sociation (Juraszek 1928) soc.nov. (Table IX, distribution map 16)

Classification: *Calluna vulgaris* soc., probably belonging to a Cladonio-Callunetum (see Krieger 1937, Passarge 1964 a, Oberdorfer et al. 1967), lacks both characteristic and differential taxa. Only a group of cryptogams, common to Salici-Empetretum, is found including *Dicranum scoparium*, *D. undulatum*, *Cladonia arbuscula* et *mitis*, *C. chlorophaea* coll. and *C. impexa*. Apart from the dominant *Calluna vulgaris* only *Hypnum ericetorum*, *Salix arenaria* and *Luzula campestris* are of high order and ranked with Vaccinio-Genistetalia and Nardo-Callunetea. The companion taxa are few, from Vaccinio-Piceetea such as *Cladonia rangiferina*, from Deschampsio-Quercetea *robori-petraeae* such as *Quercus robur* juv. and *Koelerio-Corynepherea*. Furthermore, there are some trivial cryptogams such as *Parmelia physodes* and *Brachythecium rutabulum*.

Structure: The vegetation consists of a dense to closed, double-layered dwarf shrub community, dominated by *Calluna vulgaris*, often very high-growing. The bottom layer is well developed chiefly with *Pleurozium schreberi* as a subdominant (see Osvald 1923 Table 45, Størmer 1938 Table 24) and alternating in *Cladonia* spp. *C. arbuscula* et *mitis* is most striking at Revingehed, *C. impexa* at Sandhammaren. Du Rietz, G.E. (1921 Table 11, 1925 b, 1932) has described a naked *Calluna vulgaris*-ass. (nudo-nanolignosa), where the ground layer is strongly reduced. In the lichen-rich *Calluna* heath analyzed by Krieger (1937) *Cladonia arbuscula* is most prominent. Often several grazing relicts can be found in a Cladonio-Callunetum (see Berglund 1963 Table 4 *Cladonia* var.) or various nano-ligneous plants (see Tüxen 1951 p. 159).

Development: The plant community grows on poor outwashed sands (see Tüxen 1958), certain moraines (see Osvald loc.cit.) and on rocks, especially in the coastal districts (see Du Rietz, G.E. 1932). *Calluna vulgaris* soc. or Cladonio-Callunetum is often in a

mosaic with *Cladonio-Corynephorum*, in the archipelago region an *Agrostideto-Rumicetum tenuifolii* (Tüxen 1951 Table 3), various pine forests and *Melampyro-Quercetum roboris* and sometimes borders on wet-growing vegetation (see Osvald op.cit., Jonas 1935). At Sandhammaren *Calluna* rings are seen with *Cladonia* spp. in the interspaces, bryophytes only if the climate is more hygric. *Empetrum nigrum* seems to be superseded by *Calluna vulgaris* (see Ellenberg 1963 pp. 648-649). In the dry inland of Jutland the development seems to be the reverse (Böcher 1941 a p. 88). The presence of juvenile oaks in the heather carpets is an indication of a succession to oak forests in the siliceous districts.

Ecological remarks: The ecosystem is established in strongly acid habitats. The soil type is a podsol with a well stratified A-B-C-profile, but not so pronounced as a *Genisto-Callunetum* with a marked eluvial horizon (Table XXII), with a matted, up to 5 cm thick raw humus layer. The A-horizon, largely sand with a dark humus mixture, is below 30 cm. The B-layer is a mineral soil with reddish mottling. At Sandhammaren the bed (C), with yellowish white sand, starts at 130-140 cm. The organic content is somewhat higher, about 3.7 % in the surface soil and 0.8 % in the subsoil, compared with *Salici-Empetretum Lophocolea heterophylla* subass. The soil reaction is nearly the same in the surface soil, pH 4.6 (in KCl 3.5), in the subsoil lower 5.0 (4.2).

Distribution: A plant community corresponding to a *Cladonio-Callunetum* is widely spread, although scattered, in the Middle and Northern parts of Europe (Warming 1914, Du Rietz, G.E. 1921, 1925 b, 1932, Osvald loc.cit., Juraszek 1928, Jonas op.cit., Krieger op.cit., Størmer op.cit., Atlestam 1942, Raabe 1950, Tüxen 1951, 1958, Stoutjesdijk 1959, Berglund op.cit., Passarge op.cit.). In the sub-Atlantic region transitional plant communities to *Calluno-Genistion pilosae* may be registered (Nilsson, A. 1901, Malmström 1937, Tüxen 1937 p. 121, Böcher 1941 a, 1943 a, 1970, Büker 1942 Table 16, Damman 1957, Schubert 1960 Table 17, Runge 1973). In Middle Sweden, Finland and the Baltic States (Samuelsson 1910, Steffen 1931 Table 45, Jalas 1950 Table 7, Jalas & Valpas 1961) the dwarf shrub heath with *Antennaria dioica* and *Arctostaphylos uva-ursi* forms an outpost to the boreal *Loiseleurio-Vaccinieta*. *Calluna vulgaris* soc. has been found at Revingehed and at Sandhammaren.

Sociological relationships: Juraszek (op.cit.) has proposed a *Calluna vulgaris - Cladonia silvatica - rangiferina*-ass. or *Xerocallunetum vulgaris*. Du Rietz, G.E. (1921) has reported a naked *Calluna vulgaris* -ass. and (1932) a *Calluna-Cladonia rangiferina-silvatica-soc.*, Krieger (op.cit.) a *Calluna vulgaris - Cladonia silvatica* -ass. called *Cladonio-Callunetum* (Passarge op.cit.) belonging to a *Cladonio-Callunum* prov., in Oberdorfer et al. (op.cit.) *Calluno-Genistion*. The present plant community is associated mainly with *Empetrium boreale* and *Myrtillion boreale* according to Böcher (1943), has certain affinities to a *Calluna-Vaccinium* community (Malmer et al. 1965) and is arranged into the Scano-Danish (Scotch) series (Böcher op.cit., Gimingham 1961, 1964) but seems to contain widely distributed species (de Smidt 1967) of *Vaccinio-Genistetalia* and *Nardo-Callunetea*.

Agrostio-Callunetum (Damman 1957) ass.nov. (Table X, distribution map 17)

Classification: A group of differential taxa such as *Hieracium pilosella*, *Agrostis tenuis*, *Jasione montana*, *Knautia arvensis*, *Rumex tenuifolius*, *Hieracium umbellatum*, *Viola canina*, *Cladonia rangiformis*, *Scleranthus perennis*, *Euphorbia cyparissias* and *Hypericum perforatum* characterizes *Agrostio-Callunetum*. *Calluna vulgaris*, *Hypnum ericetorum* and *Luzula campestris* are of high order and ranked with *Euphorbio-Callunum*, *Vaccinio-Genistetalia* and *Nardo-Callunetea*. *Agrostio-Callunetum* is very rich in companion taxa, from *Vaccinio-Piceetea* such as *Cladonia arbuscula et mitis* and *C. cornuta et gracilis*, from *Koelerio-Corynephoretea* such as *Agrostis canina* ssp. *montana* and *Cladonia furcata* and from a disparate group with many cryptogams such as *Pleurozium schreberi*, *Cladonia* spp., *Lophocolea heterophylla* and *Dicranum scoparium*.

Structure: The vegetation consists of a dense to closed, double-layered, dwarf shrub community, normally with *Calluna vulgaris* as the only *nano-chamaephyte*. Many herbaceous plants as well as graminides are present, both *xerophytes* and *mesophytes*. The stands are in a mosaic with various grassland communities and several relicts from *Teesdalia-Corynephorum* are of both floristical and structural importance to *Agrostio-Callunetum*, on several places high-growing, up to half a metre (see Damman 1957, Mattiasson 1971) also

somewhat shorter (see Böcher 1945 Fig. 23, Schubert 1960) as at Vomb and Flyinge and overgrown by *Agrostis tenuis*, more seldom by *Euphorbia cyparissias*. The plant community contains many thermophytes or drought indicators (Damman op.cit. p. 390). The well-developed bottom layer is marked by the presence of *Pleurozium schreberi* and *Hypnum ericetorum* and with a reduced cover of the lichens, different from the *Cladonia* variant described by Damman (op.cit.) and Mattiasson (op.cit.) from East Scania.

Development: *Agrostio-Callunetum* occurs on dry sandy soils, more rarely on flat rocks. It is of strongly anthropogenous origin and regarded a substitute of deciduous forests and thin pine forests, a secondary community (Schubert op.cit. p. 148) maintained by burning, grazing and felling. In some places the plant community may be regarded as a degenerated grass heath, *Teesdalia-Corynephoretum*, or a poor meadow, *Festuca ovina* - *Rumex acetosa* comm., in a succession to a forest (Berglund 1963 p. 65). The latter is normally an oak forest, in Scania an *Agrostio-Quercetum roboris*. The regeneration of juvenile pines from adjacent plantations can possibly also lead to pine forests.

Ecological remarks: The ecosystem is characterized by a diffusely stratified soil profile, forming a podsol-ranker and not a podsol due to the low precipitation (Damman op.cit. p. 388), probably a result of a more rapid breakdown of the organic matter compared with *Calluna vulgaris* soc. The raw humus layer is very thin. The A-horizon is normally below 25 cm, at Vitaby up to 55 cm, and consists of sand with a dark humus mixed with roots. The (B)-C-layers con-

tain a brownish mineral soil, often with a coarse material. The humus content is lower in the surface soil, about 3.0 %, and higher in the subsoil, about 1.3 %, compared with *Calluna vulgaris* soc. The soil reaction could be nearly the same, pH 4.7 (in KCl 3.7) and 4.9 (4.3) from corresponding layers. Mattiasson (1971) has given a pH-amplitude 4.1-5.0 from East Scanian *Agrostio-Callunetum*.

Distribution: In the sub-Continental and certain Continental districts of Europe *Euphorbio-Callunion* (see Schubert 1960 Karte 4) including *Agrostio-Callunetum* has replaced the sub-Atlantic *Calluno-Genistion pilosae*. Thus the split distribution of *Euphorbio-Callunion* includes the eastern parts of Denmark and Sweden (Warming 1914, Böcher 1943 a Table 13, 1945, Damman op.cit., Andersson, O. 1950 a Table 3, Berglund op.cit. Table 4 'Normaltyp', Malmer et al. 1965, Mattiasson 1970, 1971) and parts of Central Europe (Klika 1931, 1934, Knapp 1944, Schubert op.cit., Passarge 1964 a, 1964 b Table 4).

Sociological relationships: *Agrostio-Callunetum* is similar to a *Hylocomieto-Callunetum hieracietosum* (Damman op.cit.) in East Scania separated from a *Hylocomieto-Callunetum vacciniotosum* belonging to *Calluno-Genistion pilosae*. In the Böcher system *Agrostio-Callunetum* is placed into *Callunion balticum*. Schubert (op.cit. pp. 123-175) has described a *Festuca glauca* - *Calluna vulgaris* -ass (*Festuco-Callunetum*) and an *Euphorbia cyparissias* - *Calluna vulgaris* ass. (*Euphorbio-Callunetum*), both belonging to *Euphorbio-Callunion* (Schubert op.cit. pp. 206-209), and Passarge (1964 b) a *Pulsatilla-Calluna-comm.* belonging to the same



Fig. 11. *Agrostio-Callunetum* advancing over *Teesdalia-Corynephoretum*. Haväng north of Vitemölla 1973. Photo H. Olsson.

alliance from Central Europe with affinities to Agrostio-Callunetum. Also a Calluno-Genistetum with Continental plants given by Knapp (op.cit.) and a Calluneto-Genistetum medioeuropaeum (Preisling 1953 Table 4) are much more related to Euphorbio-Callunion than to the sub-Atlantic Calluno-Genistion pilosae. Passarge (1964 a) has presented five alliances within Vaccinio-Genistetalia, viz., Calluno-Genistion, Euphorbio-Callunion, Cladonio-Callunion, Empetrium boreale and Sarothamnion, Westhoff & Den Held (1969) only Calluno-Genistion pilosae and Empetrium nigri.

Rose bush vegetation

Agropyro- Rosetum rugosae (Olsson 1971) ass.nov. (Table VIII, distribution map 18)

Classification: *Rosa rugosa* is a characteristic taxon, normally a dominant, of *Agropyro- Rosetum rugosae*. *Chamaenerion angustifolium* and *Calamagrostis epigeios* are differential taxa of the association. *Carex arenaria*, *Agropyron repens* and *Deschampsia flexuosa* are among the companion taxa.

Structure: The vegetation consists of a closed, high growing single-layered plant community totally dominated by *Rosa rugosa*. Other plants are scattered. No bottom layer is formed. *Agropyro- Rosetum rugosae* on verges and in parks is similar in structure but sometimes with more nitrophilic plants.

Development: Natural *Rosa rugosa* communities are described from Japan by Ohba et al. (1973), where the *Rosa rugosa* stands are important parts in the dune succession. In Denmark (Østergaard 1953-54, Jessen 1958) and probably also in Sweden the plant was introduced in the 19th century, but it was spread more widely in the beginning of this century, being planted on the dunes in order to stop the sand shifting. The rose bushes grow solitary or in clones depressing the marram grass and forming a new nitrophilic habitat abruptly bordering on *Elymo-Ammophiletum*, less common also on *Violo-Corynephorretum*, *Salicetum arenariae* and *Salici-Empetretum*. Jessen (op.cit.) has reported *Rosa rugosa* stands near the beach on the embryo dunes.

Ecological remarks: The ecosystem forms a specific habitat on the coastal dunes. Jessen (op.cit.) has shown that *Rosa rugosa* can be spread very easily.

Distribution: *Agropyro- Rosetum rugosae* occurs on West Swedish maritime sands, from Haverdal to

Falsterbo, and along the Danish coast (see Østergaard op.cit., Jessen op.cit., Weimarck 1963 p. 391). It is also strongly anthropogenous in the inland.

Sociological relationships: The anthropogenous and weakly nitrogenous *Agropyro- Rosetum rugosae* has not earlier been classified into a phytosociological system. Following Passarge & Hofmann (1968 pp. 235-243) the association seems to be affiliated with *Urtico-Crataegion* of *Urtico-Crataegetalia* ranked with *Urtico-Sambucetea*. According to Westhoff & Den Held (1969) the related alliance could be *Berberidion* placed into *Prunetalia spinosae* (Tüxen 1952) of *Rhamno-Prunetea*. The researches of Boerbom (1960 Table 15) and Doing (1962 pp. 40-42) point out certain relationships with the *Hippophae rhamnoides* communities.

Bog myrtle vegetation

Molinio- Myricetum gale Almqvist 1929 *Salix arenaria* subass. Doing 1962 (Table XI, distribution map 19)

Classification: *Myrica gale* is a characteristic taxon of *Molinio- Myricetum gale*. *Salix arenaria* is a differential taxon of a *Salix arenaria* subass. Five variants have been differentiated. *Vaccinium uliginosum*, *Potentilla erecta* and *Festuca arenaria* belong to a *Vaccinium uliginosum* variant. *Erica tetralix*, *Cephaloziella* sp., *Peltigera malacea*, *Empetrum nigrum*, *Gymnocolea inflata*, *Calluna vulgaris* and *Luzula multiflora* are among an *Erica tetralix* var. *Sphagnum recurvum*, *Oxycoccus palustris* and *Viola palustris* are associated with an *Oxycoccus palustris* var. *Agrostis canina* and *Potentilla palustris* belong to an *Agrostis canina* var. *Lysimachia vulgaris*, *Lythrum salicaria*, and *Carex acuta* are among a *Carex acuta* var. The companion taxa are from various classes, e.g., *Parvocaricetea* such as *Carex nigra*, *Drepanocladus exannulatus* and *Calliergon cordifolium*, from *Molinio-Arrhenatheretea* such as *Galium uliginosum* and *Carex nigra* and to a lower degree also from *Phragmitetea*, *Nardo-Callunetea* and *Oxycocco-Sphagnetetea*. *Molinia coerulea* may be a dominant companion taxon.

Structure: The vegetation consists of an open to dense, double or weakly triple-layered, rather high-growing plant community (see Waldheim & Weimarck 1943 Table 3) often in pioneer stands.

The inland, typical subassociation reaches up to one metre in height, the coastal *Salix arenaria* subass. 30-60 cm. Of the ligneous plants *Myrica gale* forms a somewhat higher layer than the nano-chamaephytes *Calluna vulgaris*, *Erica tetralix*, *Empetrum nigrum*, *Vaccinium vitis-idaea* and *V. uliginosum*, normally present but in reduced frequency. The tussocky *Molinia coerulea* and *Myrica gale* are also constituents, mainly of the same height, of a weakly unstratified inland plant community (see Almquist 1929 Table 30). *Molinia coerulea* may, in certain inland stands, be reduced or absent (see Osvald 1923 pp. 109-110, Larsson, A. & Svensson 1972 Tables 2-3), but very often lacking in *Salix arenaria* subass. (see van Dieren 1934 Tables 59-62). The graminids, especially from *Parvocaricetea*, are important as structural elements. The herbs are less prominent. The ground layer may vary from sparsely to densely coated with bryophytes. *Salix arenaria* subass. is often developed as a gradient community with several variants from closed stands with *Vaccinium uliginosum* on back dunes, where *Myrica gale* is nearly lacking, scattered with plants from *Nardo-Callunetea* as *Potentilla erecta* and *Sieglingia decumbens*. On moister habitats the floristic structure is similar to that of *Ericion tetralicis* (see de Smidt 1966 pp. 160-161, Westhoff & Den Held 1969) luxuriant in *Erica tetralix* combined with the liverworts *Gymnocolea inflata* and *Cephaloziella* sp. in micro depressions surrounded by various dwarf shrubs. Also the lichen *Peltigera malacea* is confined to the *Erica tetralix* var.

On small hummocks *Molinia coerulea* and *Sphagnum recurvum* physiognomically determine the vegetation with *Oxycoccus palustris* and *Viola palustris* lying on the vaulted moss mat. On lower parts in the terrain elements from *Caricion canescens-nigrae* such as *Carex nigra* and *Agrostis canina* are mixed with *Myrica gale* and *Salix arenaria*. The bottom layer is fragmentarily composed of *Drepanocladus exannulatus* and *Calliergon cordifolium*. In the poor fens in the mire districts in Western and Middle Sweden tussocks or lawns with *Myrica gale* and *Molinia coerulea* may be present (see Sjörs 1948 Fig. 23, Malmer 1965 p. 154). In the *Carex acuta* var. the vegetation is very un-homogenous, dominated by *Myrica gale* and *Carex nigra*, with strongly reduced *Salix arenaria* and with remnants from *Caricetum acutae* as the irregular tufts of *Carex acuta* of varying height and the

presence of flowering *Lysimachia vulgaris* and *Lythrum salicaria* show. From the shores of the lake Bolmen Plejmark (1971) has described a related plant community.

Development: *Molinio-Myricetum gale* occurs on acid oligotrophic to mesotrophic sandy soils, in rather wet and periodically inundated habitats and in some places with a weak tendency to peat formation. On shores edging lakes and rivers a *Molinio-Myricetum gale* (see Almquist op.cit. p. 154, Malmer et al. 1965 p. 130) is found on the uppermost parts of the geolittoral bordering on tall shrubs of *Rhamnus frangula* and *Salix aurita* as well as of forests, mainly *Myrico-Betuletum pubescentis*. In NW Europe *Molinio-Myricetum gale* is preceded by various plant communities from *Ericion tetralicis*. *Salix arenaria* subass. is established in the non-calcareous coastal dunes in the Atlantic region, often in contact with *Salicetum arenariae*, *Salici-Empetretum*, *Caricetum canescens-nigrae*, *Caricetum acutae*, in some places also with tall shrubs of *Salix cinerea*. The vegetational succession leads to *Myrico-Betuletum pubescentis*.

Ecological remarks: The ecosystem is confined to poor minerotrophic milieus occupied by several acidophytes in a sharp gradient hygrosere. The soil type, only *Salix arenaria* subass., is a ranker developed on a moist brownish sand with a humus mixture in the surface which is difficultly penetrable by precipitation water. The humus content in the surface soil is about 3 %. The mean pH value is 5.0 (in KCl 4.2). From a typical subass. of *Molinio-Myricetum gale* Böcher (1941 a Table 58) has given a pH amplitude 3.5-4.3.

Distribution: *Molinio-Myricetum gale* is found mainly in the Atlantic or boreo-Atlantic parts of Europe (Raunkiaer 1914 Table 5, Jonas 1933 p. 80, 1935 pp. 117-119, van Dieren 1934, Meijer & Drees 1936, Böcher 1941 a, 1943 a, 1970, Hild 1960, Kop 1961, Noirfalise & Sougniez 1961 p. 281, Passarge 1961, Doing 1962, Fischer 1967, Westhoff & Den Held 1969) on the British Isles normally a mire community (Tansley 1953 p. 670, Ratcliffe 1964 Table 56). From South and West Sweden many works are published in which *Molinio-Myricetum gale* is assigned mostly to the poor fens (Osvald loc.cit., Malmström 1937 p. 426, Sjörs 1948 pp. 120-121, Waldheim & Weimarck loc.cit., Malmer loc.cit.) but also to the shore lakes and the southwestern coast

(Malmer et al. loc.cit., Nilsson, N.-G. 1966, Plejmark op.cit., Larsson, A. & Svensson op.cit., Tyler et al. 1973). In the Baltic and Bothnian region *Molinio- Myricetum gale* forms outposts, often near the sea shores (Almquist op.cit., Wangerin 1921, Lippmaa 1931 p. 66, Libbert 1940 p. 74, Havas 1961 p. 87, Wojterski 1963, Passarge & Hofmann 1968). Within the investigation area *Salix arenaria* subass. occurs at Haverdal and Tönnersa. At the first locality there is also a fragment of a typical subass. (see Nilsson, N.-G. op.cit. p. 22).

Sociological relationships: Almquist (op.cit.) has proposed a *Myrica-Molinia*-ass., synonymous to *Molinio- Myricetum gale* and shown that *Molinia coerulea* and *Myrica gale* are very closely affiliated, although Osvald (op.cit.) has separated a *Myrica gale* -ass. naked *Myrica*-heath from a *Molinia coerulea* -ass., *Molinia coerulea* meadow, more correctly a poor fen. Jonas (loc.cit.) has divided a *Myricetum sphagnosum* into *Myrica gale* - *Sphagnum recurvum* soc. and *Myrica gale* - *Molinia coerulea* - *Narthecium ossifragum* soc. Fischer (op.cit.) has described a related *Frangulo-Myricetum* with an *Erica tetralix* subass. and a *Peucedanum palustre* subass., the latter has agreements with a lake shore community reported by Plejmark (op.cit.). Doing (op.cit.) has described a *Salix arenaria* subass. bound to the non-calcareous dunes. A *Myrico-Salicetum cinereae* (Passarge op.cit.) from NW Germany or a *Myrica* comm. (Noirfalise & Sougniez op.cit.) from Belgium marked with the presence of tall shrubs such as *Salix cinerea*, *S. aurita* and *Rhamnus frangula* in combination with *Myrica gale* has not been registered within the investigation area. Passarge & Hofmann (op.cit.) have distinguished two regional alliances, *Eu-Molinio-Frangulion* in the temperate Central Europe and a boreo-Atlantic *Molinio- Myricion gale*, both belonging to *Molinio-Frangulion* with relationships to *Salicion auritae* (Doing op.cit.) and *Salicion cinereae* (Müller & Görs 1958). The order *Salicetalia auritae* (Doing op.cit.) corresponds only partly to *Rubo-Franguleta* prov. (Passarge & Hofmann op.cit.). Müller & Görs (op.cit.) separated the tall shrubs from *Alnetea glutinosae*. Doing (op.cit.) placed the acidophilic shrubs into *Franguletea*, changed to *Betulo-Franguletea* with narrower limits (Passarge & Hoffmann op.cit.).

The *Myrica-Molinia* vegetation complex has taken an intermediate position between heath and mire

vegetation (see Böcher 1941 a, 1943 a, Waldheim & Weimarck op.cit., Sjörs op.cit., Malmer op.cit., Malmer et al. op.cit.). There is also a gradient between *Ericion tetralicis* (see de Smidt 1966, Westhoff & Den Held op.cit. p. 233, Malmer et al. 1965, Tyler et al. op.cit.) and *Molinio- Myricion gale*. Furthermore, a *Myrica-Molinia* combination has structural importance in wet-growing pine and birch forests.

Molinio- Myricetum gale Almquist 1929 *Molinia coerulea* socation Osvald 1923 (Table XI, distribution map 20)

Classification: *Molinia coerulea* is a differential dominant of *Molinia coerulea* soc. *Dicranum scoparium*, *Hypnum cupressiforme* coll., *Brachythecium rutabulum* and *Deschampsia flexuosa* are among the companion taxa.

Structure: The vegetation consists of a dense and high-growing tussocky, mainly single-layered plant community physiognomically determined by *Molinia coerulea* (see Osvald 1923 p. 147, Böcher 1941 a Table 34:1-4). The plant community can also be uniformly double-layered (see Jonas 1935 pp. 35-42, Mörnjö 1969 Table 13).

Development: The *Molinia coerulea* soc. occurs on acid sandy soil in the siliceous landscape with dwarf shrubs, poor oak forests and various mire forests with *Betula pubescens* and *Pinus sylvestris* (see Fukarek 1961 Table 3). At Sandhammaren the present plant community is often in contact with *Calluna vulgaris* soc.

Ecological remarks: The ecosystem seems to be confined to depressions in the terrain, where the soil type is a transitional stage between a podsol and a peaty soil. The humus layer, black and matted, probably forms an anmoor (Duchafour 1970 p. 159).

Distribution: *Molinia coerulea* soc. (Osvald loc.cit., Jonas loc.cit., Böcher loc.cit., Fukarek loc.cit., Mörnjö loc.cit.) has a wider distribution than *Molinio- Myrica gale* due to a transition to *Molinietum coeruleae* (Koch 1926), especially in the Baltic region (Kobendza 1930, Pastak 1936-37 Table 9, Libbert 1940, Albertson 1946 Table 34, Fröde 1957-58). Within the investigation area *Molinia coerulea* soc. has been found only at Sandhammaren.

Sociological relationships: A *Molinia coerulea* soc. is connected both with *Molinio- Myricetum gale*

(Osvald loc.cit., Böcher loc.cit.) and with *Molinietum coeruleae* (Pastak loc.cit., Albertson loc.cit.) but also with a *Betuletum pubescentis* (Fukarek loc.cit.) and with a *Molinio-Quercetum roboris* (Tüxen 1937 p. 129, Passarge & Hofmann 1968). Thus *Molinia coerulea* soc. could belong to at least four disparate classes, viz., *Betulo-Franguletea*, *Molinio-Arrhenatheretea*, *Molinio-Betuletea pubescentis* and *Deschampsio-Quercetea roboris-petreae*.

Forest and shrubby wood vegetation

Pine vegetation

Cladonio-Pinetum sylvestris Kobendza 1930 em. Passarge 1956 (Table XII, distribution map 21)

Classification: *Cladonia arbuscula* et *mitis* (only the first one), *C. impexa*, *C. cornuta* et *gracilis* (both) and *C. rangiferina* are characteristic taxa of *Cladonio-Pinetum sylvestris* and *Cladonio-Pinion*. *Cladonia rangiferina* also marks a typical subassociation separated from a *Corynephorus* subass. with *Corynephorus canescens*, *Cornicularia aculeata*, *Carex arenaria*, *Cladonia furcata* and *Polytrichum piliferum*. In the latter subassociation a *Galium verum* variant with *Galium verum* and *Ammophila arenaria* is found. *Pinus sylvestris* and *Dicranum undulatum* are of high order and ranked with *Vaccinio-Piceetalia* and *Vaccinio-Piceetea*. *Pleurozium schreberi*, *Dicranum scoparium*, *Cladonia chlorophaea* coll. and *Deschampsia flexuosa* are prominent companion taxa. Many occasional plants of minor importance are present.

Structure: The vegetation consists of an open, double or weakly triple-layered plant community with coniferous phanerophytes, normally only *Pinus sylvestris*. The pines are scattered in light stands, 10–15 m high and upright with rather small crowns. Maritime stands may be lower and shrubby with *Pinus mugo* and *P. sylvestris* richly branched, not exceeding 5 m. Also a related plant community on rocks, a 'hällmarkstallskog' (see Sterner 1926 p. 106, Sjörs 1967 p. 126) is sparsely formed. The ground is covered with lichens and less strikingly also with bryophytes. The frequency and number of plants may be highly variable (see Krieger 1937). Of the *Cladonia* spp. *C. impexa* seems to be the most com-

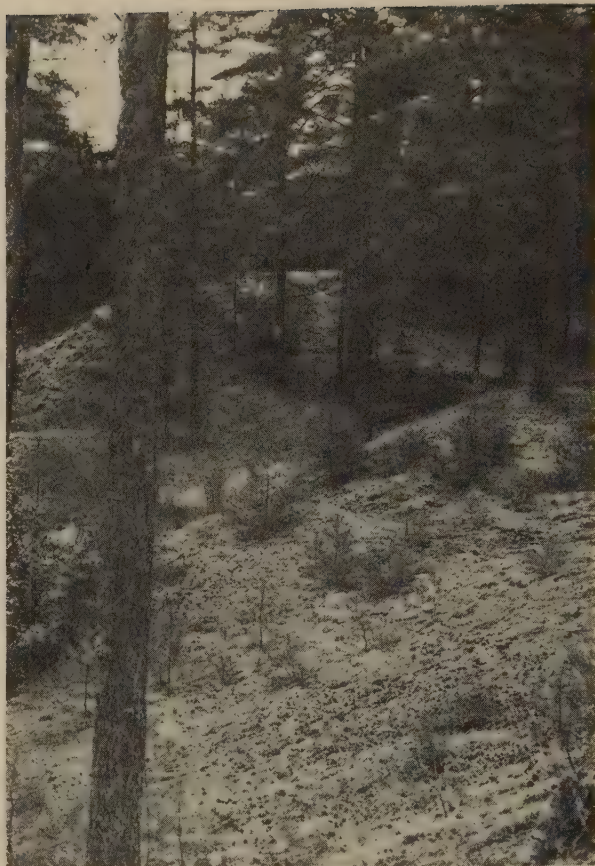


Fig. 12. *Cladonio-Pinetum sylvestris* typical subass., on the old dunes ca. 3 km from the seashore at Tönnersa 1973. Photo B. Wallén.

mon one, also in afforestations (see Køie 1938, Table XIII). Old stands are physiognomically determined by *C. rangiferina*, *C. arbuscula* and to the north also by *C. alpestris*. The last-mentioned has its southernmost locality in Sweden at Furuboda. It normally grows in a mosaic with patches of dwarf shrubs (Tamm, O. 1937, Sjörs loc.cit.) which is similar to a *Cladonio-Pinetum boreale* (Cajander 1921). In the *Corynephorus canescens* subass. plants from *Koelerio-Corynephoretea* have structural importance forming a weakly developed field layer, in the shrubby variant also with *Ammophila arenaria* and richer in bryophytes and with resemblance to the 'grasreiche Kieferngehölze' from the Gulf of Finland (see Passarge & Passarge 1971 Table 2). The planted closed stands with shrubby *Pinus mugo* are lacking in the field layer and with only a badly developed ground layer.

Development: According to Kielland-Lund (1971) the lichen pine forest is common on shallow soil often with infertile glaci-fluvial material in the dry

lowland regions. *Cladonio-Pinetum sylvestris* occurs mainly on poor, dry, old sand dunes, in South Sweden scattered in the coastal districts. In the inland, except some Boreo-nemoral forests in the province of Småland, *Cladonio-Pinetum sylvestris* is absent or nearly lacking, different from the Continental forests on glacial sand. The occurrences along the South Swedish coasts seem to be natural but not original, which is the case in the SE Baltic (Kobendza 1930, Fukarek 1961 p. 123, Wojterski 1964 b Table 13), but they are not affiliated with the strongly anthropogenous planted pine stands, *Pseudopinetum sylvestris*. *Cladonio-Pinetum sylvestris* is regarded to be a relatively short stage in a succession towards *Vaccinio-Pinetum sylvestris* or *Melampyro-Quercetum roboris* and preceded by a *Cladonio-Corynephorum* and a *Calluna vulgaris* soc. always adjacent.

Ecological remarks: The ecosystem is recognized by an extremely poor growth due to reduced water content, with a mini-deficiency of bases and minerals, which results in rather open habitats. The soil type is a podsol in the typical subassociation with sharply bordered horizons with a thick eluvial layer above a pan (see Tamm, O. op.cit. Fig. 5, Kundler 1961 Abb. 1) and a podsol-ranker in the *Corynephorus canescens* subass. with a low humus content.

Distribution: Lichen-rich pine forests occur in the boreal and Continental districts of Europe. In the Atlantic parts they are reduced and only isolated on places with suitable environmental conditions (Warming 1916-19 p. 590, Køie op.cit. p. 28). In the boreal parts vicariant communities are present (Cajander op.cit., Almquist 1929 p. 313, Tamm, O. op.cit., Jalas 1950 pp. 139-141, Kujala 1961, Kielland-Lund 1967, 1971, Sjörs loc.cit.) somewhat different from *Cladonio-Pinetum sylvestris* in the Nemoral Europe (Preuss 1911-12 p. 98, Krieger op.cit., Passarge 1956 a, 1956 b, 1957, 1962 a, 1968, Fukarek loc.cit., Matuszkiewicz 1962, Hofmann 1964, Wojterski op.cit., Passarge & Hofmann 1968, Klemm 1969-70, Krausch 1970). In the eastern parts between the Nemoral and boreal regions *Arctostaphylos uva-ursi* is often an important participant in *Cladonio-Pinetum sylvestris*, also in the northern vicariant *Cladonio-Pinetum boreale*, forming a specific plant community (Juraszek 1928, Kobendza op.cit., Steffen 1931, Regel 1944, Braun-Blanquet et al. 1939 p. 67, Matuszkiewicz op.cit.,

Passarge & Passarge 1971). In Middle Europe (Knapp 1942, Obendorfer 1957, Hohenester 1960, Ružička 1961, Zeidler & Straub 1967) there are south vicariant communities. Also certain related lichen-rich *Pseudopinetum sylvestris* may be mentioned (Meisel-Jahn 1955, Scamoni 1961 Table 10, Hofmann 1969 p. 409). Within the investigation area *Cladonio-Pinetum sylvestris* is found at Tönnersa, Sandhammaren and Furuboda, on all localities both the typical subassociation and *Corynephorus canescens* subass.

Sociological relationships: Juraszek (op.cit. Table 2) has reported a *Pineto-Cladinetum* and Kobendza (op.cit. Table XI) a *Pineto-Cladonietum* changed to *Cladonio-Pinetum sylvestris* (Passarge 1956 a, 1956 b), placed into a *Cladonio-Pinion* with three regional alliances (Passarge 1968, Passarge & Hofmann 1968), viz., the boreal *Cetrario-Pinion sylvestris* partly embracing *Phylodoco-Vaccinion* (see Braun-Blanquet et al. op.cit., Kielland-Lund 1967), with *Cladonio-Pinetum boreale* (Cajander 1921, Kielland-Lund 1967, 1971), the Central European *Eu-Cladonio-Pinion sylvestris* on lowlands and *Cetrario-Pinion hercynicae* on highlands. Libbert (1933) has separated a *Pinion medioeuropaeum*, in Oberdorfer (1957) named *Pinion* and in Matuszkiewicz (op.cit.) *Dicrano-Pinion*, in which *Leucobryo-Pinetum cladonietosum* is correspondent both to a typical lowland race and a coastal race, according to Wojterski (1964 b) *Empetro nigri-Pinetum cladonietosum*. Passarge & Hofmann (op.cit.) has pointed out a western *Cladonia impexa* race, probably also in South Sweden, and an eastern *Carex ericetorum* race. Fukarek (op.cit.) has separated a *Corynephorus canescens* subass. from a typical one, also valid in South Sweden. A *Corynephorum-Pinetum sylvestris* reported in Olsson (1971) is changed into a *Cladonio-Corynephorum Corynephorus canescens* subass. The lichen-rich forests belong to *Vaccinio-Piceetalia* (Braun-Blanquet et al. op.cit.), the regional order *Vaccinio-Pinetalia sylvestris* (Passarge 1968) of *Vaccinio-Piceetea* (Braun-Blanquet et al. op.cit.).

Vaccinio-Pinetum sylvestris Kobendza 1930 em. Passarge 1956 (Table XIII, distribution map 22)

Classification: *Hylocomium splendens* is a local characteristic taxon of *Vaccinio-Pinetum sylvestris*. *Empetrum nigrum* is a differential taxon of an



Fig. 13. *Vaccinio- Pinetum sylvestris* *Empetrum nigrum* subass. Furuboda 1973. Photo. H. Olsson.

Empetrum nigrum subass. *Quercus petraea* and *Picea abies* belong to a *Quercus petraea* subass. In the first subassociation *Calluna vulgaris*, *Parmelia physodes* and *Cladonia arbuscula et mitis* form a *Calluna vulgaris* variant. *Dicranum undulatum* is a characteristic taxon of *Vaccinio-Pinion*. *Pinus sylvestris*, *Vaccinium vitis-idaea*, *V. myrtillus* *Cladonia arbuscula et mitis* (only the first one), *C. impexa*, *C. rangiferina*, *Ptilium crista-castrensis* and *Trientalis europaea* are of high order and ranked with *Vaccinio-Piceetalia* and *Vaccinio-Piceetea*. *Pleurozium schreberi*, *Carex arenaria*, *Hypnum cupressiforme* coll., *Brachythecium rutabulum*, *Dicranum scoparium* and *Scleropodium purum* are prominent companion taxa.

Structure: The vegetation consists of a dense to closed, triple-layered, plant community with various phanerophytes, besides the often dominating pine, also spruce and birch. The pines are chiefly high-growing, upright with small crowns and, in mature stands, of the same height and age. In certain light stands the regeneration of juvenile pines is very good and the structure may be somewhat different with an irregular tree layer and with *Calluna vulgaris* as a subdominant and in some places also with *Cladonia* spp. (see Du Rietz, G.E. 1921, Arwidsson 1938, Regel 1944 Table IV, Hofmann 1964) often with a well-developed moss layer (Køie 1938 Table VII, Regel op.cit. Table V, Jonsson 1957, Fukarek 1961 Table 18). As a rule, the most important nanochamaephytes in the moraine landscape are *Vaccinium vitis-idaea* and *V. myrtillus* (Du Rietz, G.E. op.cit., Malmström 1937 p. 388, Tamm, O. 1937,

Køie 1938 Tables V-VI, Tamm, C.-O. 1947, Størmer 1938, Passarge 1956 b, Fukarek loc.cit.). The bottom layer is composed largely of pleurocarpic mosses such as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*. The acrocarpic mosses are represented by *Dicranum scoparium*, *D. undulatum* and further to the north also *D. fuscescens*. The last-mentioned one is together with the lichen *Peltigera aphthosa* of structural importance in some boreal forests. In stands with spruces in majority the plant community has been more closed and according to Kielland-Lund (1967 p. 136) the lichens and the *Dicrano-Pinion* (syn. *Vaccinio-Pinion*) plants are depressed. The coastal *Vaccinio- Pinetum sylvestris* in South Sweden is in general poor in *Vaccinium myrtillus*, which is common on morainic soils. The *Empetrum nigrum* subass. is characterized by a rather low canopy of the pines and with a combination of *Carex arenaria* and *Empetrum nigrum* on the ground, also with interspaces in the vegetation (see Libbert 1940, Wojterski 1964 b). Sometimes there is a mosaic between dwarf shrubs, forming phases (see Fukarek loc.cit.). It is striking that *Empetrum nigrum* can grow well both in rather shady places as under the branches and in light open stands. An extremely dry habitat at Haverdal has formed a specific vegetation with *Empetrum nigrum* carpets in a mosaic with patches of *Cladonia* spp. forming a transitional stage to *Cladonio- Pinetum sylvestris* (see Wojterski op.cit. Table 13). The *Quercus petraea* subass. has a resemblance to the inland moraine *Vaccinio-Pinetum sylvestris* with pines mixed with *Picea abies*,

Betula pubescens and *Quercus petraea*. *Vaccinio-Pinetum sylvestris* on maritime sands is poor in plants, especially herbs. Also the trivial *Trientalis europaea* and *Melampyrum pratense* are uncommon. The boreal element *Linnea borealis* is very rare.

Development: *Vaccinio-Pinetum sylvestris* occurs on poor sandy plains or moraines, on dry or moist ground. On rocks with a shallow soil the forest is only fragmentary. On dry drained mires there is also a related vegetation; according to Almquist (1929) a *Vaccinio-Pinetum* developed from a *Ledo-Pinetum* is nearly identical to a terrestrial forest. Osvald (1923) has described coniferous communities both on moraines and peaty soils. Within the investigation area the pine forests on the dunes are for the most part of secondary origin occupying parts of *Melampyro-Quercetum roboris*, possibly original on certain sites at Furuboda and then bordering on *Cladonio-Pinetum* and *Pyrolo-Pinetum* (see Tüxen 1951 p. 164). In *Salici-Empetretum Lophocolea heterophylla* subass. the pine regeneration seems to be superior to the oak and a development to a *Vaccinio-Pinetum sylvestris Empetrum nigrum* subass. may be maintained, near the sea for a long time. Landwards *Melampyro-Quercetum* seems to supersede *Vaccinio-Pinetum* in the subsera from *Cladonio-Corynephorum*, via *Calluna vulgaris* soc. to a climax forest in normal succession not interrupted by man. *Vaccinio-Pinetum* can also be in contact with *Deschampsia flexuosa - Pinus sylvestris* comm. and on moister ground also with *Myrico-Betuletum pubescentis*. The succession on the dunes is somewhat different compared with the conditions in the moraine landscape, where planted spruce forests can disturb the development.

Ecological remarks: The ecosystem is associated with a strong raw humus formation due to the continuous supply of remnants from various ligneous plants, especially pine needles favoured by the precipitation. Also the local climate, highly variable, is important. The slowly decomposed, acid raw humus contributes to the leaching often facilitated by a good permeability. The effect of the ground water is trivial, although certain stands are bound to moist habitats. The soil type is a podsol, in the *Empetrum nigrum* subass. in some places also a podsol-ranker (see Wojterski op.cit. Fig. 8, Fukarek op.cit. Fig. 20), with a thick raw humus layer normally followed by a

sharp horizon with pale sand in SW Sweden very obvious (see Tamm, O. 1937 Figs. 5-6). The eluvial zone lies on a distinct illuvial B-layer mottled with iron concretions giving a reddish colour down to about 50 cm, on the moraines (see Table XXII) and certain glaci-fluvial sands still deeper to 100 cm (see Jonson op.cit. p. 420). The coastal pine forest in South Sweden seems to lack a pan in the B-layer, as can be seen in the soil profiles of a *Pineto-Empetretum nigri* presented by Piotrowska (1960 Figs. 25-26) and not uncommon in SW Swedish inland (see Tamm, O. op.cit. p. 12). The organic matter in the raw humus, where roots are abundant can exceed 80 % in the inland, but is low on the coast varying from about 5 % in *Empetrum nigrum* subass. to about 25 % in *Quercus petraea* subass. In the subsoil, 50-60 cm, the differences in the humus content are not so pronounced, about 0.7 % along the coast, 1-3 % on the moraines. The soil reaction from various *Vaccinio-Pinetum* in South Sweden seems to be similar, pH 4.0-4.5 at 0-10 cm (in KCl 2.8-3.8) and at 50-60 cm a mean value of 4.8 (4.3). The grain size is strongly variably from well-sorted aeolian sand (*Quercus petraea* subass.), or the occurrence of fine shingle (*Empetrum nigrum* subass.) at Haverdal, to the stony moraines also with fine fractions in the inland.

Distribution: The main area of *Vaccinio-Pinetum sylvestris* is boreal to sub-Continental, occupying the Scandinavian peninsula and the South and East Baltic parts up to Finland. The forests is only fragmentary in Western and Southern Europe (Warming 1916-19 p. 592, Køie op.cit. pp. 17-21, Størmer 1938 Tables 19-20, Tansley 1953, Oberdorfer 1957, Westhoff 1959 Table II, Hohenester 1960, Kielland-Lund 1967 p. 137, Zeidler & Straub 1967, Westhoff & Den Held 1969). The boreal vicariant, *Vaccinio-Pinetum boreale*, reaches south to the province of Småland in Sweden and eastward to the Baltic States (Hesselman 1908, Cajander 1921, Du Rietz, G.E. 1921, 1925 Table 2, Osvald op.cit., Sterner 1926 p. 103, Almquist op.cit., Linkola 1929, Regel 1928, 1944, Tamm, O. 1937, Tamm, C.-O. 1947, Jalas 1950, Jonsson op.cit., Pettersson 1958, Kujala 1961, Sjörs 1965 pp. 56-57, Kielland-Lund 1967, 1971, Passarge & Passarge 1971). The Central European *Vaccinio-Pinetum sylvestris* is common in West Poland, DDR and southernmost Sweden (Preuss 1911-12 pp. 99-100, Juraszek 1928 Table 3, Kobendza 1930 Table 14,

Hueck 1932, Libbert 1933, Braun-Blanquet et al. 1939, Malmström op.cit., Piotrowska 1955, Passarge 1956 b, 1957, Schubert 1960, Scamoni 1961 Table 11, Matuszkiewicz 1962, Hofmann 1964, Passarge & Hofmann 1968, Klemm 1969-70, Krausch 1970) and along the coast as *Empetrum nigrum* subass. (Malmström 1939 pp. 225-230, Libbert op.cit., Månsson 1960 p. 361, Piotrowska 1960, Wojterski 1964 a, 1964 b, Fukarek op.cit.). In the East Baltic parts and on the islands of Öland and Gotland and probably in certain pine forests in East Scania there is a *Peucedano-Pinetum* rich in herbs and graminids (Du Rietz, G.E. 1925 d, Sterner loc.cit., Juraszek 1927 Table 3, Kobendza 1930 Table 10, Steffen 1931 pp. 79-89, Regel 1944, Matuszkiewicz 1962, Pettersson 1958, Kielland-Lund 1967). On less poor habitats a *Pyrolo-Pinetum sylvestris*, according to Passarge & Hofmann (op.cit. p. 211) rather identical to the previous association, with scattered distribution (Preuss loc.cit., Warming 1914 p. 286, Libbert op.cit. p. 65, Meusel 1951 p. 229, Fukarek op.cit. Table 19, Kujala op.cit., Passarge & Hofmann loc.cit.), only at Ängelholm and Furuboda (see Tüxen 1951 p. 164) within the investigation area, in which *Vaccinio-Pinetum sylvestris Empetrum nigrum* subass. has been registered from Haverdal to Ängelholm, at Sandhammaren and Furuboda, *Quercus petraea* subass. only at Haverdal.

Sociological relationships: *Vaccinio-Pinetum sylvestris* has been divided into an inland *Myrtillo-Vaccinio-Pinetum* (Juraszek op.cit., Kobendza op.cit., Passarge 1956 b) and into a coastal *Empetro-Vaccinio-Pinetum* (Libbert 1940, Piotrowska op.cit., Wojterski 1964 b). Passarge & Hofmann (loc.cit.) have pointed out a regional association with *Picea abies*, *Ptilium crista-castrensis* and *Hylocomium splendens*. In the division made by Matuszkiewicz (op.cit.) *Leucobryo-Pinetum*, also with a coastal race, *Peucedano-Pinetum* and *Empetro-Pinetum fenoscandium* are vicariant associations. There is no reason to distinguish a separate coastal *Empetro nigri-pinetum*, with four subassociations according to Wojterski (1964 b), similar to the present *Empetrum nigrum* subass., also agreeing in some respects with a *Pinetum myrtilletosum* (Hueck op.cit.) and *Myrtillo-Pinoquercetum empetrosum* (Fukarek op.cit.). Meusel (op.cit.) has proposed a *Pyrolo-Pinetum*, split into a *Empetro-Pyrolo-Pinetum* and a *Peucedano-Pyrolo-Pinetum* (syn.

Peucedano-Pinetum) according to Passarge & Hofmann (loc.cit.). Both *Vaccinio-Pinetum* and *Pyrolo-Pinetum* belong to a *Vaccinio-Pinion* together with *Cladonio-Pinion* embracing *Dicrano-Pinion* (Libbert 1932-33, Matuszkiewicz op.cit.). *Vaccinio-Pinion* has been separated into the boreal *Empetro-Pinion sylvestris* containing *Vaccinio-Pinetum boreale* (Cajander op.cit., Kielland-Lund 1967, 1971), the Nemoral *Vaccinio-Pinion sylvestris* and the southern montane *Vaccinio-Pinion hercynicae* (see Passarge & Hofmann op.cit.). In the division made by Braun-Blanquet et al. (op.cit.) *Vaccinio-Piceion* is separated into several suballiances, e.g., *Piceion septentrionale* including *Pineto-Vaccinietum myrtilli*, within the Eurosibiric region of *Vaccinio-Piceetalia* and *Vaccinio-Piceetea* (syn. *Betuleto-Pinetea* Knapp 1942) on mesophilic places different from a *Uliginosi-Pinetea* on wet habitats and the termophilic Continental *Erico-Pinetea*.

Deschampsia flexuosa - Pinus sylvestris community Steffen 1931 (Table XIII, distribution map 23)

Classification: *Deschampsia flexuosa* is a local differential taxon of a *Deschampsia flexuosa - Pinus sylvestris community*. Two variants have been distinguished. *Lophocolea bidentata* belongs to the first one. *Melampyrum pratense*, *Polypodium vulgare* and *Luzula campestris* are among the second one. *Dicranum undulatum* is a characteristic taxon of *Vaccinio-Piceion*. *Pinus sylvestris*, *Vaccinium vitis-idaea*, *V. myrtillus* and *Trientalis europaea* are of high order and ranked with *Vaccinio-Piceetalia* and *Vaccinio-Piceetea*. *Pleurozium schreberi* is a dominant companion taxon. *Carex arenaria*, *Brachythecium rutabulum* and *Scleropodium purum* are also among the companion taxa.

Structure: The vegetation consists of an open to dense, triple-layered plant community, poor in species. The physiognomy is determined by *Deschampsia flexuosa*, in closer stands reduced in number and with a more prominent bryophyte layer. *Pleurozium schreberi* and *Dicranum undulatum* are most abundant. *Carex arenaria* occurs scattered, also in similar forests in the Vomb plain, in some places together with *Trientalis europaea* and *Melampyrum pratense*. Structural agreements with the *Deschampsia flexuosa - Stadium* (Fukarek 1961 Table 20) and with the *Deschampsia flexuosa soc.* (Køie 1938 Table 9) are found, but often without *Lonicera periclymenum* and with less *Scleropodium*

purum. Also a pine afforestation reported by Paul (1953 Table 34) is related, where a mixture of *Pleurozium schreberi*, *Scleropodium purum* and *Hylocomium splendens* may be seen. Of interest is a *Linnaea borealis* phase (Steffen 1931 p. 90), sparse at Sandhammaren.

Development: *Deschampsia flexuosa* - *Pinus sylvestris* comm. is a transitional stage between natural pine forests (see Steffen loc.cit.) and afforestations (see Køie loc.cit.), in this work not regarded a typical *Pseudopinetum* (see Hofmann 1969), according to Fukarek (op.cit. p. 134) without rank, and only a 'Stadium' in a development from *Pyrolo-Pinetum* to a climax forest. Sometimes this pine plant community has been planted on dwarf shrub heaths and is often in contact with *Calluna vulgaris* soc. or *Agrostio-Callunetum* and in some places in a mosaic with various forests as *Cladonio-Pinetum*, *Vaccinio-Pinetum*, *Melampyro-Quercetum* and *Agrostio-Quercetum* as well as with different *Pseudopinetum*.

Ecological remarks: The ecosystem is characterized by a thick raw humus on a sandy soil with a very acid reaction, more acid than other coniferous forests according to Steffen (loc.cit.). The soil type is a podsol. The A-layer, sand with a humus mixture, is below 25 cm. The B-horizon is mottled and brownish. At Sandhammaren there are also second A- and B-layers. The C-zone starts at 100-120 cm, where the colour of the mineral soil is yellowish. The humus content in the surface soil is high, at 0-5 cm at Sandhammaren about 55 % in the subsoil low, at Furuboda about 0.3 %. The average pH is 4.0 (in KCl 2.9) at 0-5 cm, very closely corresponding to the figures given by Køie (loc.cit.) and Steffen (loc.cit.). In the subsoil the pH is lower at Sandhammaren than at Furuboda, in C-layer 4.9 (4.2) and 5.5 (4.5) respectively. The grain size is a well-sorted sandy fraction.

Distribution: A vegetation corresponding to the *Deschampsia flexuosa* - *Pinus sylvestris* comm. has been described from several places in the South Baltic area (Regel 1928, Steffen loc.cit., Libbert 1940 p. 69, Meusel 1951, Paul loc.cit., Fukarek op.cit.). Strongly anthropogenous forests, related to *Pseudopinetum sylvestris*, are registered by Køie (loc.cit.), Meisel-Jahn (1955 p. 55), Scamoni (1961), Passarge (1962), Hofmann (1964, 1969), Klemm (1969-70) and Ljungberg & Persson, Y. (1973).

Within the investigation area this type of forest has been found at Sandhammaren, Furuboda and in some places in the Vomb plain.

Sociological relationships: The *Deschampsia flexuosa* - *Pinus sylvestris* comm. seems to be more affiliated with *Vaccinio-Pinion*, also shown by the researches by Steffen (loc.cit.), than to *Deschampsio flexuosae* - *Pseudopinetum* with four 'Elementargesellschaften' in a system of afforested pine forests proposed by Hofmann (1969).

Oak vegetation

Agrostis tenuis - *Populus tremula* community comm.nov. (Table XIV, distribution map 24)

Classification: *Populus tremula*, as a tall shrub, is a characteristic dominant of the *Agrostis tenuis* - *Populus tremula* comm. *Lophocolea bidentata*, *Agrostis tenuis* and *Rubus idaeus* are differential taxa towards an *Oxalis acetosella* - *Quercus petraea* comm. and *Melampyro-Quercetum roboris*. *Maianthemum bifolium*, *Populus tremula* juv., *Sorbus aucuparia* juv., *Melampyrum pratense* and *Quercus robur* juv. are of high order and ranked with *Melampyro-Quercion*, *Melampyro-Quercetalia* and *Deschampsio-Quercetea robori-petraeae*. *Deschampsia flexuosa*, *Brachythecium rutabulum* and *Lysimachia vulgaris* are the most prominent companion taxa.

Structure: The vegetation consists of a dense to very closed double or weakly triple-layered tall shrub community. *Populus tremula* is often the prevalent phanerophyte. In some places at Furuboda *Salix caprea* may be a subdominant in the tall shrub layer, normally 2-4 m high, also with scattered *Rhamnus frangula*. Various intermediate-growing shrubs are present such as *Myrica gale*, *Rubus idaeus* and *Rosa* spp. *Deschampsia flexuosa* is mainly predominant in the field layer, in very closed stands superseded by *Maianthemum bifolium*, also seen in the aspen forest from the island of Gotska Sandön (Arwidsson 1938). In open light stands *Deschampsia flexuosa* may be replaced by *Agrostis tenuis*. *Lophocolea bidentata* is striking in the poorly developed bottom layer.

Development: The acidophilic deciduous *Agrostis tenuis* - *Populus tremula* comm. grows on poor sandy soils, possibly also on moraines and rocks. In the maritime districts the aspen canopies are formed by the winds (see Warming 1909 Figs. 84-85),

streamlined on the backdunes, often in contact with Elymo-Ammophiletum, Violo-Corynephorum and Salici-Empetretum and different wet-growing vegetation. In the inland aspen shrubs may be seen in the margin of oak and birch forests (cf. Passarge & Hofmann 1968 p. 254) forming an instable zone.

Ecological remarks: The ecosystem is located in oligotrophic habitats on undeveloped acid soils, podsol-ranker or podsol, with only a thin humus layer in the surface.

Distribution: Very little is known about the range of an *Agrostis tenuis* - *Populus tremula* comm. along the coasts (see Warming 1909) and in the inland (Warming 1916-19 p. 80, Passarge & Hofmann loc.cit.). The plant community has been found on the west coast from Haverdal to Ängelholm as well as at Furuboda on the Baltic coast.

Sociological relationships: Tüxen (1951) has distinguished a Querceto- *Populetum tremulae* (syn. *Melampyro- Quercetum roboris*) from South Scandinavia including the *Agrostis tenuis* - *Populus tremula* comm. Also Gram et al. (1944) and Ivarsson (1962) have placed the aspen shrubs under various oak forests belonging to *Melampyro-Quercion*, *Melampyro-Quercetalia* and *Melampyro-Quercetea robori-petraeae*. In the system made by Doing (1962) and Passarge & Hofmann (loc.cit.) the plant community, in Olsson (1971) called *Agrostio-Populetum tremulae*, belonging to an *Agrostio-Populion tremulae* (Passarge & Hofmann loc.cit.), could belong to a *Betulo-Franguletea* (syn. *Franguletea*).

Oxalis acetosella - *Quercus petraea* community comm.nov. (Table XIV, distribution map 25)

Classification: *Quercus petraea* and *Sorbus aucuparia* are characteristic taxa of an *Oxalis acetosella* - *Quercus petraea* comm. *Oxalis acetosella*, *Anemone nemorosa*, *Fragaria vesca*, *Poa nemoralis* and *Brachythecium velutinum* are differential taxa towards *Melampyro- Quercetum roboris* and the *Agrostis tenuis* - *Populus tremula* comm. *Melampyrum pratense*, *Convallaria majalis*, *Sorbus aucuparia* juv., *Populus tremula* juv., *Maianthemum bifolium* and *Solidago virgaurea* are of high order and ranked with *Melampyro-Quercion*, *Melampyro-Quercetalia* and *Deschampsio-Quercetea robori-petraeae*. *Lysimachia vulgaris* is one of the few companion taxa.

Structure: The vegetation consists of a dense to closed, double or weakly triple-layered plant community. The tree layer can be divided into two: a 15-20 m high *Quercus petraea* coating, as well as a lower *Sorbus aucuparia* of 10 m in height. The stems are very upright. The oak trunks are thick, rather scattered as the result of the clearance. Various tall shrubs are missing but may be adjacent. In the field layer *Oxalis acetosella* and *Convallaria majalis* are predominant, in the spring aspect mainly *Anemone nemorosa*, resembling a *Quercus robur* comm. on loamy ground reported by Andersson, F. (1970 Table 5). The ground layer is reduced or lacking. Compared with other coastal oak communities the herbs are in the majority and *Deschampsia flexuosa* less common. The appearance of *Lysimachia vulgaris* and *Fragaria vesca* points to certain affinities to oak forests on moist ground on the moraines.

Development: An *Oxalis acetosella* - *Quercus petraea* comm. is at Haverdal situated behind the ancient inner dunes near the arable land. On the dune ridge the vegetation is poorer, like a *Melampyro-Quercetum roboris* though the dominating tree is *Quercus petraea*, and with the presence of *Tilia cordata* and *Juniperus communis* rather related to a *Quercus petraea* - *Deschampsia flexuosa* comm. from the province of Blekinge (Berglund 1963 Table 1).

Ecological remarks: The ecosystem with many mesophytes is associated with a moderately acid soil forming a podsoloid with a raw humus up to 5 cm and the A-horizon, sand mixed with humus, exceeding 20 cm diffusely transformed into the B-C-layers, yellowish brown in colour. At 0-5 cm the humus content is 12 %, at 50-60 cm only 0.6 %. Corresponding pH values are 4.7 (in KCl 3.8) and 5.1 (4.1) respectively. The grain size >0.2 mm is 86 %.

Distribution: Very little is known about the range of an *Oxalis acetosella* - *Quercus petraea* comm. Plant communities physiognomically determined by *Quercus petraea* are reported from various places in Europe (Braun-Blanquet & Tüxen 1952, Tansley 1953, Oberdorfer 1957, Passarge 1957, Jones 1959, Neuhausl & Neuhauslová-Novotná 1967, Passarge & Hofmann 1968), in South Sweden (Weimarck 1947 c, Berglund loc.cit.).

Sociological relationships: An *Oxalis acetosella* - *Quercus petraea* comm. is related to *Melampyro-*

Quercetum roboris belonging to *Melampyro-Quercion*, also comparable to richer deciduous forests. In this investigation the present community is placed into *Melampyro-Quercetalia*, though there are small points of contact also with *Molinio-Quercetalia* (Passarge & Hofmann op.cit.), of *Deschampsio-Quercetea robori-petraeae*.

Melampyro-Quercetum roboris R.Tx. (1930) 1937 em. Passarge & Hofmann 1968 (sub nom. *Querceto roboris - Betuletum typicum* R.Tx. 1930) *Calamagrostis epigeios* vicariant Doing 1962 (Table XIV, distribution map 26)

Classification: *Calamagrostis epigeios* is a differential taxon of a coastal vicariant of *Melampyro-Quercetum roboris* (inland vicariant with *Vaccinium vitis-idaea*). Three subassociations have been distinguished: a typical one without differential taxa, a second one with *Corylus avellana* and *Rhamnus frangula* and a third one with *Corynephorus canescens*, *Cladonia chlorophaea* coll., *Cornicularia aculeata* and *Polytrichum piliferum*. The typical subassociation is split into five variants: *Betula verrucosa* of the first one, *Luzula campestris* and *Anthoxanthum odoratum* of the second one, *Vaccinium myrtillus* of the third, *Pteridium aquilinum* of the fourth, *Peucedanum oreoselinum* and *Vicia cassubica* of the fifth. *Melampyrum pratense*, *Convallaria majalis*, *Quercus robur*, *Sorbus aucuparia* juv., *Populus tremula* juv., *Maianthemum bifolium*, *Solidago virgaurea*, *Betula verrucosa*, *Pteridium aquilinum*, *Lonicera periclymenum*, *Lathyrus montanus* and *Rubus saxatilis* are of high order and ranked with *Melampyro-Quercion*, *Melampyro-Quercetalia* and *Deschampsio-Quercetea robori-petraeae*. *Deschampsia flexuosa*, *Brachythecium rutabulum* and *Poa pratensis* are among the companion taxa, as well as *Carex arenaria* and *Campanula rotundifolia* from *Koelerio-Corynephoretea*.

Structure: The vegetation consists of a dense to closed normally triple-layered plant community with various xerophytes and mesophytes. The tree layer is dominated by *Quercus robur* and often with *Betula verrucosa* as a participant or in the coastal districts also *Populus tremula* (see Tüxen 1951 pp. 157-159). *Quercus petraea* may be mixed (see Ivarsson 1962, Berglund 1963). The inland heath oak forests are often marked with the presence of *Vaccinium vitis-idaea* and *V. myrtillus* (see Malmström 1937, Linnermark 1960) and the presence of

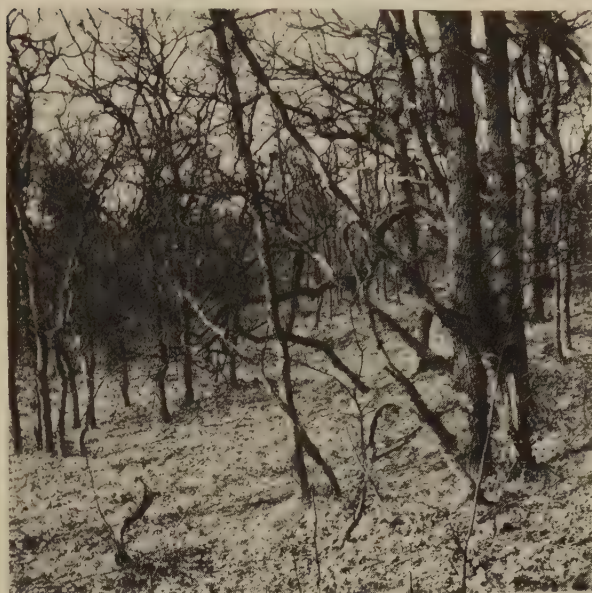


Fig. 14. *Melampyro-Quercetum roboris Calamagrostis epigeios* vicariant typical subass. An oak stand in winter. The ground is covered with leaf litter. During the vegetation period *Deschampsia flexuosa* and *Convallaria majalis* are predominant. Sandhammaren 1973. Photo B. Wallén.

Calamagrostis epigeios is striking in the forest on maritime sands at Sandhammaren and the southernmost part of the island of Öland. Nearest the sea *Betula verrucosa* woods can be seen, 2-4 m high, with a field layer dominated by *Melampyrum pratense*, *Calamagrostis epigeios*, *Deschampsia flexuosa* and *Carex arenaria*, but very reduced in *Convallaria majalis*. *Brachythecium rutabulum* is an important bryophyte. In the *Luzula campestris* var. (see Olsen 1938 Table 8), with 5-10 m high oaks, the vegetation is monotonous, in the field layer physiognomically determined by *Convallaria majalis* and *Deschampsia flexuosa*. On north sides of the dune ridges *Vaccinium myrtillus* is in some places predominant and together with *Maianthemum bifolium* characterizes a very acidophilic vegetation poor in plants (see Böcher 1942 Table 1:18-19). In certain stands *Pteridium aquilinum* covers the ground above the normal field layer dominated by *Convallaria majalis* and *Deschampsia flexuosa*. The phanerophyte layer is composed of upright, 10-20 m high, scattered trees of oaks and aspens in rather light stands. The trees are more than 80 years old. *Pteridium aquilinum*, an aestival species of the upper field layer (Tansley 1953 p. 286) is very common in poor oak woods on sandy soils (see Warming 1916-19 pp. 521-530, Olsen op.cit., Böcher loc.cit., Gram

et al. 1944) illustratively shown in the *Periclymeno-Quercetum pteridetosum*, also with pines (Piotrowska 1960). In the variant with the Continental termophytes *Peucedanum oreoselinum* and *Vicia cassubica* the frequencies of *Melampyrum pratense* and *Calamagrostis epigeios* have decreased. The oaks are lower, scattered and with broader crowns.

In stands with *Corylus avellana* the stratification is another. Below the tree layer with high thick oaks well-developed tall shrubs, mainly *Corylus avellana* and *Rhamnus frangula*, about 3 m high, are clustered. The sub-Atlantic element *Lonicera periclymenum* is creeping on the ground as well as climbing on the trees. In the coastal oakwoods on Jutland the combination of *Corylus avellana* and *Lonicera periclymenum* is very common (see Gram et al. op.cit.). The plants in the field layer are common to the typical subassociation without the occurrence of *Anemone nemorosa*. In certain stands the ground is naked or sparsely covered with *Maianthemum bifolium*. In the third subassociation, very different from the previous, the oaks are creeping or shrubby and scattered termophytes from *Koelerio-Corynephoretea* are present. A related oak vegetation can be seen in Warming (1909 pp. 139-146).

Development: *Melampyro-Quercetum roboris* is an acidophilic forest in the siliceous districts on shallow soils, chiefly on the moraines but also on different sands. According to Tüxen (1951 p. 158) the same *Quercetum-Populetum tremulae* is regarded a paraclimax, replaced by *Querceto-Ulmetum* on loamy soils. The area of *Melampyro-Quercetum roboris* is anthropogenously influenced, somewhere degenerated to a dwarf-shrub heath often planted with *Pinus sylvestris*. In some places, the forests, in a mosaic with meadows (see Berglund op.cit. pp. 40-41), may be utilized for grazing; on other places isolated among coniferous forests and mires. In the vegetational succession on maritime dunes, the final stage is a natural potential forest (Tüxen 1967 b p. 174), in NW Europe mainly composed of *Quercus robur* and in the East Baltic and Bothnian Bay districts of *Pinus sylvestris*. The coastal *Melampyro-Quercetum roboris Calamagrostis epigeios* vicariant is preceded by *Salici-Empetretum*, in the Atlantic region also of a *Hippophaeto-Salicetum arenariae* (see Klement 1953 Table 8). In the closing of the vegetation *Melampyro-Quercetum roboris* is the

final stage in a development from *Cladonio-Corynephoretum* via *Calluna vulgaris* soc. Pine forests and birch-fen forests may be in contact as well as *Agrostio-Quercetum roboris*.

Ecological remarks: The ecosystem is normally confined to poor, acid, dry habitats without or with very little influence from the ground water. The dominating soil type is podsol, although more rarely the ecosystem may be associated with a podsoloid and an oligotrophic brown earth (see Linnermark op.cit.). On the moraines in SW Sweden the podsol is very pronounced with an obvious E-horizon between the A- and B-layers and a thick raw humus layer, which in the *Melampyro-Quercetum roboris Calamagrostis epigeios* vicariant is more diffusely transformed into a sandy humus layer of varying depth. The B-horizon is a brownish mottled sand. At Sandhammaren the uneffected bed lies below the second A- and B-layers, in the *Luzula campestris* var. about 160 cm deep. There is a pan at about 50 cm in the *Pteridium aquilinum* var. In *Corynephorus canescens* subass. the soil type is a podsol-ranker. The humus content in the surface soil can exceed 30 %, in the inland vicariant often 80 %, in the *Corynephorus canescens* subass. only 0.5 %, at 50-60 cm about 1 %. The mean value of pH in the raw humus layer of the typical subass. is 4.1 (in KCl 3.1) and 4.6 (3.8) at 50-60 cm agreeing with corresponding figures from the moraines with Scanian *Quercus petraea* forests (see Weimarck 1947 c). In *Corylus avellana* subass. the soil reaction seems to be the same while the pH is higher in *Corynephorus canescens* subass. The grain size is strongly variable, in *Vaccinium myrtillus* var. the fraction 0.6-0.2 mm is totally dominating.

Distribution: *Melampyro-Quercetum roboris* occurs in the Eurosibirc flora region in Western and Central Parts of Europe up to South Sweden, along the Swedish west coast and southernmost Norway and is important in Denmark. The western forests is characterized by the presence of *Lonicera periclymenum* (Warming 1919, 1916-19, Christiansen 1925, Meijer Drees 1936, Tüxen & Diemont 1936, Tüxen 1937, 1951, 1967 a Table 7, Vlieger 1937, Olsen op.cit., Sissingh 1941, Böcher op.cit., Gram et al. op.cit., Tansley op.cit., Passarge 1956 b, 1962 a, Jones 1959, Boerbom 1960, Doing 1962, Ivarsson op.cit., Hallberg & Ivarsson 1965, Feilberg 1968, Bakker 1969, Westhoff & Den Held

1969), according to Passarge & Hofmann (1968 p. 171) a sub-Atlantic 'Periclymenum-Regionale', which probably also could be found along the South Baltic coast but mixed with pine (Piotrowska 1955, 1960, Fukarek 1961). In the Baltic and Continental Europe the oak forests sometimes contain pine (Arwidsson 1938, Oberdorfer 1957, Passarge 1957 Table IX, Linnermark op.cit., Schubert 1960 Table 4, Ottoson 1965, Neuhäusl & Neuhäuslová-Novotná 1967, Sjörs 1967 p. 122, Passarge & Hofmann 1968, Runge 1973). The *Quercus petraea* forests, Melampyro- *Quercetum petraea* (see Tüxen 1937, Passarge & Hofmann op.cit.), occur in the sub-Atlantic-sub-Continental area of Europe and often together with beeches and pines besides *Quercus robur* (Tüxen 1937, Passarge 1957, Scamoni 1961, Müller & Stoll 1968, Passarge & Passarge op.cit., Zeidler & Straub 1967). They occur in Sweden too (Malmström op.cit., Weimarck 1947 c, Berglund 1963, Andersson, E. & Nilsson, J.A. 1970). Within the investigation area Melampyro- *Quercetum roboris* *Calamagrostis epigeios* vicariant is found only at Sandhammaren. In the innermost part of the sands at Ängelholm there is an inland vicariant.

Sociological relationships: Doing (1962 p. 67) has proposed a *Querco-Betuletum* (syn. Melampyro-*Quercetum roboris*) *Calamagrostis epigeios* vicariant. A *Convallario-Quercetum dunense* (Boerbom 1960, Doing 1962, Westhoff & Den Held op.cit.) must not be confused with it, although certain similarities with a *Betula verrucosa* var. of Melampyro- *Quercetum roboris* are found. Bakker (1969) has separated a *Maianthemo-Quercetum*, including the *Convallaria*-rich stands, from *Querceto-Betuletum*, which Tüxen (1937) divided into a *Quercus robur* subass. group and a *Quercus sessiliflora* subass. group, both with a typical and a *Molinia coerulea* subass. In the system of Passarge & Hofmann (op.cit.) these units have been changed to Melampyro- *Quercetum roboris*, Melampyro-*Quercetum petraeae*, *Molinio-Quercetum roboris* and *Molinio-Quercetum petraeae* respectively. The original *Quercion robori-petraeae* has in Doing (1962, 1963) been separated into *Violo-Quercion* and *Vaccinio-Quercion* belonging to one order *Quercetalia robori-petraeae* (Tüxen 1937, 1955), in Passarge & Hofmann (op.cit.) both the alliance and the order have been split. The orders are *Dicrano-Quercetalia*, *Molinio-Quercetalia* and Melampyro-

Quercetalia, the last one with Melampyro-*Quercion* and *Agrostio-Quercion*. All acidophilic oak forests are included in *Deschampsio-Quercetalia robori-petraeae* (see Braun-Blanquet & Tüxen 1943 in Passarge & Hofmann op.cit.) well separated from *Vaccinio-Piceetalia* in structure and physiognomy, combined by Knapp (1942) to *Betuleto-Pinetea*, although in East Europe mixed forests also occur.

Agrostio-Quercetum roboris (Passarge 1953) Passarge & Hofmann 1968 (Table XV, distribution map 27)

Classification: A group of differential taxa such as *Agrostis tenuis*, *Veronica chamaedrys*, *Galium verum*, *Achillea millefolium*, *Anthriscus sylvestris*, *Dactylis glomerata*, *Hypericum perforatum*, *Viola riviniana* and *Galeopsis tetrahit* characterizes *Agrostio-Quercetum roboris*. *Geranium sanguineum*, *Linaria vulgaris* and *Corylus avellana* belong to a *Geranium sanguineum* variant, *Festuca rubra*, *Anthoxanthum odoratum* and *Luzula campestris* to a *Festuca rubra* variant and *Poa pratensis*, *Rhamnus frangula* and *Betula verrucosa* to a *Poa pratensis* variant. *Quercus robur*, Melampyrum *pratense*, *Lonicera periclymenum*, *Solidago virgaurea*, *Hieracium umbellatum*, *Populus tremula* juv. and *Sorbus aucuparia* are of high order and ranked with *Agrostio-Quercion*, Melampyro-*Quercetalia* and *Deschampsio-Quercetalia robori-petraeae*. *Deschampsia flexuosa* as well as *Carex arenaria* and *Campanula rotundifolia* from *Koelerio-Corynephoretea* are among the companion taxa.

Structure: The vegetation consists of an open to dense, double or weakly triple-layered plant community dominated by *Quercus robur*, in some places also together with other phanerophytes such as *Betula verrucosa* and *Fagus sylvatica*, but almost without *Populus tremula* contrary to Melampyro-*Quercetum roboris*. Herbs and graminids are predominant in the field layer as a rule without nanophytes. The number of mesophytes (see Iversen 1936 Table 33) is much higher compared with Melampyro- *Quercetum roboris* richer in xerophytes. The ground layer is poorly developed with scattered bryophytes. The combination of *Agrostis tenuis* and *Deschampsia flexuosa* is typical, in several stands more common than *Agrostis tenuis* and *Festuca ovina*. At Björka an oak-beech woodland contains *Rubus idaeus* and several mosses

cover the ground. At Sandhammaren the *Geranium sanguineum* variant represents a margin vegetation near a thermophilic deciduous forest on the slope of the esker Kåsebergaåsen.

Development: *Agrostio-Quercetum roboris* occurs normally on glaci-fluvial sandy soils, often in the arable field landscape. Somewhere the forest is degenerated to *Teesdalia-Corynephorum* or *Agrostio-Callunetum*. In normal succession on certain places *Agrostio-Quercetum roboris* seems to be replaced by a *Querceto-Ulmetum* (see Tüxen 1951). The oak-hazel-wood is of another origin and different in floristic structure (see Sjörs 1967). Certain afforested pine forests as well as *Melampyro-Quercetum roboris* may be in contact with *Agrostio-Quercetum roboris*.

Ecological remarks: The ecosystem is located in dry, rather mesophilic habitats forming a weakly developed podsol or a podsoloid, probably also an intermediate brown earth (see Linnermark 1960 pp. 102-103). In stands with much *Deschampsia flexuosa* a thin raw humus is present, in *Agrostis tenuis* stands only sand with a humus mixture diffusely followed by a B-horizon lying on a bed of yellowish sand at 25 cm. In the first type of stands the A-layer is mottled. The humus content in the surface soil is about 5 %, much lower compared with *Melampyro-Quercetum roboris*, at 50-60 cm about 1 %. The pH average is somewhat higher, in the surface 4.7 (in KCl 3.8) and in the subsoil 4.9 (4.2), compared with *Melampyro-Quercetum roboris* although the soil reaction in the *Deschampsia* stands is related. From one stand at Hemmestorp 85 % of the grain size is >0.2 mm.

Distribution: *Agrostio-Quercetum roboris* occurs mainly in the Central European lowland (Iversen loc.cit., Steffen 1936, p. 217, Olsen 1938, Gram et al. 1944, Passarge 1957, 1962 a, Doing 1962, 1963, Feilberg 1968, Passarge & Hofmann 1968, Bakker 1969 Table 2), with a western outpost on the British Isles (Tansley 1953 p. 287) and a northern outpost in Sweden (Linnermark 1960 p. 102, Ivarsson 1962, Berglund 1963 Table 1, Sjögren 1964 p. 16). *Agrostio-Quercetum roboris* has been found on several places in the Vomb plain and also at Sandhammaren.

Sociological relationships: In Sweden *Agrostio-Quercetum roboris* has agreements with a somewhat richer oak forest with *Melica uniflora*, *Stellaria*

holostea and often with *Tilia cordata* (see Berglund loc.cit., Sjögren loc.cit.). On the Continent it belongs to a *Fago-Quercetum* (see Tüxen 1955, Westhoff & Den Held 1969). According to Passarge & Hofmann (op.cit.) *Agrostio-Quercion*, belonging to *Melampyro-Quercetalia*, is split into two regional alliances *Agrostio-Quercion roboris* and *Agrostio-Quercion petraeae* both embracing a *Violo-Quercion* (Doing 1962, 1963, Bakker 1969).

Alder carr and alder meadow vegetation

Irido-Alnetum glutinosae Doing 1962 (sub nom. *Carici elongatae-Alnetum* W. Koch 1926 em. R.Tx. et Bodeux 1955) (Table XVI, distribution map 28)

Classification: *Solanum dulcamara* and *Carex elongata* are characteristic taxa of *Irido-Alnetum glutinosae* and *Irido-Alnion glutinosae*. *Iris pseudacorus*, *Peucedanum palustre* and *Lycopus europaeus* are differential taxa towards *Filipendulo-Alnetum glutinosae*. *Sphagnum recurvum* and *Potentilla palustris* belong to a *Potentilla palustris* subass. *Mnium punctatum*, *Cardamine amara*, *Caltha palustris*, *Myosotis caespitosa* and *Pellia epiphylla* are associated with a *Mnium punctatum* subass. *Alnus glutinosa*, *Calamagrostis canescens*, *Sphagnum squarrosum* and *Stellaria longifolia* are of high order and ranked with *Irido-Alnetalia glutinosae* and *Carici-Alnetea glutinosae*. Many companion taxa are present from *Molinio-*



Fig. 15. *Irido-Alnetum glutinosae Mnium punctatum* subass. Ängelholm 1973. Photo B. Wallén.

Arrhenatheretea such as *Lysimachia vulgaris*, from Phragmitetea such as *Galium palustre*, *Carex acuta* and *Naumburgia thyrsiflora* and from Parvocaricetea such as *Calliergon cordifolium*. Furthermore, *Betula pubescens* and the bryophytes *Calliergonella cuspidata*, *Mnium hornum* and *Chiloscyphus pallescens* are important companion taxa. Also many occasional plants are registered.

Structure: The vegetation consists of a dense to closed, irregularly stratified, normally triple or in certain cases quadruple-layered, hygrophilic plant community. The predominant layer in the alder carr is the phanerophyte cover rich in *Alnus glutinosa* and with reduced *Betula pubescens*. The alder reaches its optimal occurrence in Irido- Alnetum glutinosae although common in various ash forests. The field layer is physiognomically determined by the presence of robust *Iris pseudacorus* and various spp. from Magnocaricion (see Steffen 1931 p. 126, Böcher 1942 p. 15, Matuszkiewicz et al. 1958 p. 28) giving the community a hygrophilic character. Species from adjacent contact vegetation, normally meadows, include a group of mesophytes, reduced in vitality. In eutrophic habitats the degree of cover for the herbs may be higher than for the graminids (see Hueck 1934, Passarge 1957 Table II, Konczak 1968, Horst et al. 1968) compared with poorer stands (see Almquist 1929 Table 67, Christiansen 1938 Abb. 91, Sjörs 1967 Fig. 87) often with grassy tussocks. Between the field and tree layers sometimes a fragmentary tall shrub layer may be seen. In the ground layer the bryophytes prefer somewhat drier patches, often the tussocks. The interspaces are naked or in the *Potentilla palustris* subass. covered with *Sphagnum* spp. A microsera of bryocommunities is found on the alder hummocks with a quite different vegetation compared with the interspaces, thus forming a vegetation complex. On the wettest ground aquatic plants such as *Utricularia vulgaris* and *Hottonia palustris* form a structural unit sometimes called *Hottonia-Alnetum* (see Vallin 1925, Fukarek 1961 Table 40). On the driest stands *Urtica dioica*, *Rubus idaeus* and *Dryopteris austriaca* form an *Urtica-Alnetum* (Vallin op.cit., Fukarek loc.cit.). In the analyzed intermediate Irido- Alnetum glutinosae plants from these flank communities are less common. The structure of *Potentilla palustris* subass. is related to certain alder carrs on the moraines, where *Carex acuta* is lacking. *Mnium punctatum* subass. seems to be affiliated with

coast and shore lakes (see Kielland-Lund 1971 pp. 18-19).

Development: Alder carrs occur on places rather rich in nutrients with stagnant or weakly flowing water in poor oligotrophic to meso- and eutrophic habitats on hydromorphous aue soils or peaty soils, more rarely on mineral ground. Irido- Alnetum glutinosae is regarded a final stage in a hygrosera, the eutrophic subsera, often preceded by Magnocaricetalia communities such as *Caricetum acutae* and as a rule in a mosaic with different tall shrubs from *Carici-Salicetalia cinereae*. In some places other deciduous forest such as *Myrica-Betuletum pubescentis*, *Athyrium-Betuletum pubescentis* and *Filipendula-Alnetum glutinosae* may be in contact. On dry habitats the grassy tussocks and the alder hummocks are less pronounced forming a rather uniform field layer characterized by *Rubus idaeus* or transformed into an *Athyrium-Alnetum glutinosae*. On wet places the alder hummocks are large and the interspaces are brownish, naked or overgrown with *Hottonia palustris*. Malmström (1937) has described alder-birch forests on wet ground in terrain depressions similar to an *Athyrium-Alnetum glutinosae* or *Sphagnum-Alnetum glutinosae* (see Passarge & Hofmann 1968) in a mosaic with various mire vegetation.

Ecological remarks: The ecosystem is dependent on the fluctuating water inundation. The ground water table is high and during long periods of the year the interspaces are filled with water, poor in oxygen and rich in allochthonous humus. The rate of humification determines the character of the soil, peaty or mineral, brown or black, acid or neutral. The rate of humification is more rapid and the nitrogenous content is probably higher in *Mnium punctatum* subass. compared with *Potentilla palustris* subass. The soil type in the analyzed stands is regarded as aue soil, in the second subass. possibly a thin, fen peat soil. The A-horizon, about 10 cm, is formed of highly decomposed humus lying directly on the brownish mineral soil. The organic matter is about 35 % at 0-10 cm. The pH average is 6.1 (in KCl 5.4). From stand at Tönnersa the grain size >0.2 mm is about 100 %.

Distribution: Irido- Alnetum glutinosae shows little interregional variation (see Bodeux 1955, Passarge & Hofmann op.cit., Kielland-Lund 1971) and extends from Ireland to Russia covering small parts of Scandinavia. From Western Europe the following

works may be mentioned: Warming 1916-19 pp. 471-476, Tüxen 1937, Meijer Drees 1936, Vlieger 1937, Christiansen 1938 pp. 97-98, Böcher 1942, Lebrun et al. 1949, Oberdorfer 1953, 1957, Tansley 1953 p. 466, Bodeux op.cit., Maas 1959, Lohmeyer 1960, Géhu 1961 Table 26, Kop 1961, Noirfalise & Sougnez 1961, Doing 1962, 1963, Westhoff & Den Held 1969, Runge 1973. In Central and Eastern Europe several works treat the alder carr forest (Koch 1926 p. 132, Steffen loc.cit., Hueck op.cit., Klika 1939/40, Libbert 1940, Piotrowska 1955, 1960, Passarge 1956 a, 1956 b, 1957, Matuszkiewicz et al. op.cit., Neuhäusl 1959, Fukarek 1961, Horst et al. loc.cit., Konzak loc.cit., Krausch loc.cit., Passarge & Hofmann op.cit., Klemm 1969-70, Passarge & Passarge 1972 Table 15). From the Scandinavian peninsula there are few works (Du Rietz, G.E. 1925 c, Vallin 1925, Almquist loc.cit., Sjörs loc.cit., Mörnjö 1968, Kielland-Lund op.cit., Plejmark 1971). Within the investigation area Irido-Alnetum glutinosae is found at Tönnersa and Ängelholm, on the first locality only *Mnium punctatum* subass. At Haverdal landwards in the margin of the dune area an alder carr very influenced by man occurs.

Sociological relationships: The analyzed Irido-Alnetum glutinosae *Potentilla palustris* subass. has agreements with a *Betula pubescens* subass. (Bodeux op.cit. Table 6, Krausch op.cit. Table 8:3-10) and a Comaro-Irido-Alnetum (Passarge & Hofmann op.cit.). *Mnium punctatum* subass. is similar to a *Ranunculus repens* subass. (Bodeux loc.cit.), a typical subassociation (Fukarek op.cit.) and a *Pellietosum epiphyllae* (Maas op.cit. Bijlage 5). Bodeux (op.cit.) has described four vicariant associations, viz., the Euatlantic-sub-Atlantic Carici laevigatae-Alnetum, the sub-Atlantic- sub-Continental Carici elongatae-Alnetum medioeuropaeum with a north border in South Sweden, the subboreal Carici elongatae-Alnetum boreale in NE Europe and the Continental Dryopterido cristatae-Alnetum, probably only a variant of the second regional association. In the present work Irido-Alnetum glutinosae, with a western Periclymenum-Regionale and an eastern *Carex acutiformis*-Regionale (Passarge & Hofmann op.cit. p. 36) also includes Hottonio-Alnetum and Urtico-Alnetum (see Fukarek loc.cit.) as well as a Lycopo-Alnetum (Kielland-Lund op.cit.). Doing (1962) introduced Irido-Alnetum and Sphagno-Alnetum, based on structural

and ecological aspects, instead of a Carici elongatae-Alnetum of an Alnion glutinosae belonging to Alnetalia glutinosae and Alnetea glutinosae (Braun-Blanquet & Tüxen 1943, Tüxen 1955). Müller & Görs (1958) split the tall shrubs of Alnetea glutinosae into a specific class separated from Alnetalia glutinosae communities, according to Passarge & Hofmann (op.cit.) divided into Irido-Alnetalia glutinosae with Irido-Alnion glutinosae and Calamagrostio-Alnetalia glutinosae with Sphagno-Alnion glutinosae and Athyrio-Alnion glutinosae arranged into Carici-Alnetea glutinosae (syn. Alnetea glutinosae).

Filipendulo-Alnetum glutinosae (Lemée 1937) Passarge & Hofmann 1968 (sub nom. Macrophorbio-Alnetum, Lemée 1937, Maas 1959) (Table XVI, distribution map 29)

Classification: *Lythrum salicaria*, *Scutellaria galericulata*, *Rubus caesius*, *Viburnum opulus* and *Humulus lupulus* are differential taxa of Filipendulo-Alnetum glutinosae. *Anemone nemorosa*, *Athyrium filix-femina*, *Ranunculus auricomus* and *Paris quadrifolia* are among Geranio-Fraxinetea and Carpino-Fagetea (syn. both Quercu-Fagetea). The most important companion taxon is the dominant *Alnus glutinosa* as well as *Filipendula ulmaria*, moreover a differential dominant towards Irido-Alnetum glutinosae. Various other plants from Molinio-Arrhenatheretea such as *Lysimachia vulgaris*, *Deschampsia caespitosa* and *Valeriana sambucifolia* are also companion taxa as well as *Betula pubescens*, *Galium palustre*, *Viola palustris* and *Brachythecium reflexum*.

Structure: The vegetation consists of a dense to closed plant community of three or four layers. *Alnus glutinosa* is the predominant phanerophyte, *Betula pubescens* in subordination. *Fraxinus excelsior* and *Prunus padus* may be present. The alders are tall and upright, forming a closed canopy. Often the nano-phanerophytes *Rhamnus frangula*, *Viburnum opulus*, on other stands also *Evonymus europaeus* and *Corylus avellana* are present (see Sterner 1926 p. 129, Passarge & Hofmann 1968 Table 5). The field layer is composed of mesophytes and hygrophytes. Hemichryptophytes and geophytes are in majority (see Géhu 1961 p. 279). *Filipendula ulmaria* is often uniformly spread in the stands. Sometimes tufts of high individuals of *Athyrium filix-femina* can lead to a pronounced hete-

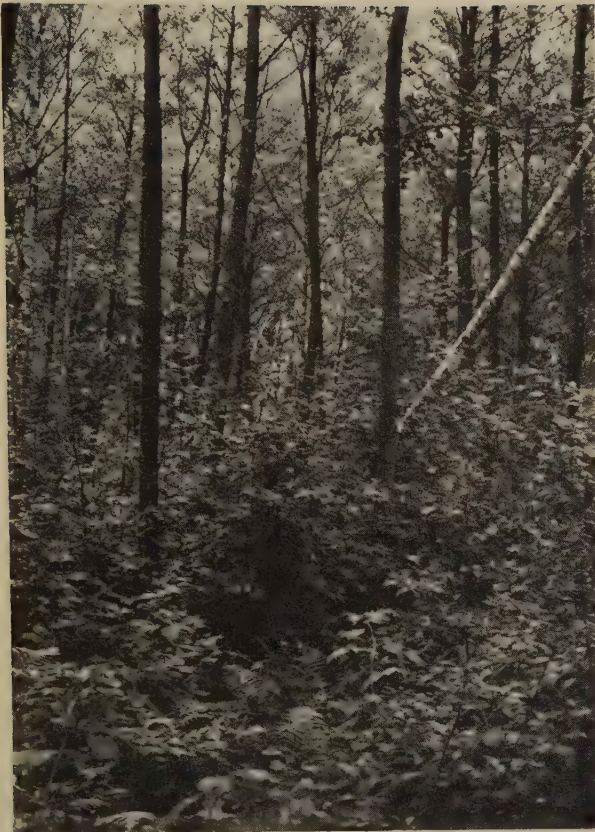


Fig. 16. *Filipendulo- Alnetum glutinosae*. *Viburnum opulus* among the tall shrubs. Tönnersa 1973. Photo B. Wallén.

rogenousness. Also *Rubus caesius* is of structural importance occupying large parts. Certain stands can be very rich in herbs such as *Valeriana sambucifolia*, *Lythrum salicaria* and *Scutellaria galericulata* and pteridophytes leading to the name *Macrophorbio-Alnetum* (see Lemée op.cit. Table 107, Maas 1959 Bijlage 6, Sterner loc.cit., Tyler 1969 Table 8). Almquist (1929 Table 68) and Andersson, L. (1971 Table III) have presented analyzes in which *Alnus glutinosa* and *Filipendula ulmaria* are a very dominant combination. Elmquist (1967) has on the Scanian moraines distinguished five variants physiognomically determined by *Fraxinus excelsior*, *Phalaris arundinacea*, *Ranunculus repens*, *Geum rivale* and *Lastrea phaeopteris* all lacking *Rubus caesius*, *Lythrum salicaria* and *Valeriana sambucifolia* found in the analyzed coastal stand. Typical of *Filipendulo- Alnetum glutinosae* is the spring aspect with *Anemone nemorosa*. The ground layer is sparsely covered by bryophytes as *Brachythecium reflexum*.

Development: *Filipendulo- Alnetum glutinosae* oc-

curs on alluvial wet soil in the lowland near rivers and lakes, in the moraine depressions and along the coasts. On many sites the plant community is strongly influenced by man through draining, clearance and grazing. The earlier wide areas occupied by alder carr forests (see Ellenberg 1963 p. 369, Sjös 1967 p. 163) are now reduced and to certain extent covered with *Filipendulo- Alnetum glutinosae*. The black alder has migrated to new habitats in richer deciduous forests (Ellenberg op. cit. p. 374) of various *Fagetalia* communities (*Geranio-Fraxinetea*) and thrives better than in the original *Carici- Alnetea glutinosae*. *Filipendulo- Alnetum glutinosae* may be in contact with *Irido- Alnetum glutinosae* (see Warming 1916-19 p. 476, Böcher 1942 p. 16), sometimes also *Athyrio- Alnetum glutinosae* (see Malmström 1937 pp. 400-401) and *Sphagno- Alnetum glutinosae* (see Malmström loc.cit., Elmquist op.cit.) as well as various ash forests with *Milium effusum* and *Carex remota* (see Lohmeyer 1960 pp. 44-55, Géhu op.cit. pp. 271-276, Passarge & Hofmann op.cit. pp. 41-59). Shore forests are, furthermore, adjacent to *Carici- Salicetea cinereae*. *Filipendula ulmaria* meadows can be seen in the vicinity (see Vallin 1925, Andersson, F. 1970).

Ecological remarks: The ecosystem is characterized by a rapid turnover and litter decomposition. The soil type is a pseudogley or where the humification is very strong a gley (A-G-profile). The specific ecological conditions are also indicated by the many nitrophytes of the vegetation. A studied pseudogley (A-S-C-profile) on wet loamy sand shows a sandy hydromull <20 cm, dark sand with a humus mixture <35 cm (A), S 35-55 cm brownish sand with iron spots and the bed C >55 cm with water. The organic matter in the surface soil is about 20 %, much lower compared with *Athyrio- Alnetum glutinosae* with about 60 %. The pH at 0-10 cm is 5.1 (in KCl 4.4), an intermediate position between *Irido- Alnetum glutinosae* *Mnium punctatum* subass. 6.1 (5.4) and *Athyrio- Alnetum glutinosae* 4.2 (3.6).

Distribution: *Filipendulo- Alnetum glutinosae* occurs in the western parts of Europe as well as the sub-boreal and sub-Continental area up to South Finland, further northwards replaced by *Alnus incana* forests also rich in herbs and pteridophytes (Warming loc.cit., Meijer Drees 1936 Table IX, Tüxen 1937 pp. 163-164, Lemée loc.cit., Böcher loc.cit., Lebrun et al. 1949 p. 191, Tansley 1953 p. 466,

Oberdorfer op.cit., Maas 1959, Lohmeyer 1960, Géhu op.cit., Fukarek 1961 Table 40, Kop 1961, Doing 1962, 1963, Noirfalise & Sougnez 1961, Passarge & Hofmann op.cit., Ellenberg loc.cit., Westhoff & Den Held 1969 pp. 265-266). The following works are from Middle and South Sweden: Vallin op.cit., Sterner loc.cit., Almquist loc.cit., Tyler loc.cit., Elmquist op.cit., Andersson, L. 1971. Within the investigation area small stands of Filipendulo-Alnetum glutinosae occur near the outlets of the small rivers at Haverdal and Tönnersa.

Sociological relationships: Macrophorbio-Alnetum (Lemée loc.cit., Maas loc.cit.), Querceto-Caropinetum filipenduletosum (Tüxen 1937, Lebrun et al. loc.cit., Géhu op.cit.), Pruneto-Fraxinetum (Oberdorfer 1953 pp. 49-51), Cirsio-Alnetum (Noirfalise & Sougnez op.cit. Table IV) are all related to Filipendulo-Alnetum glutinosae (Passarge & Hofmann op.cit.) also with certain agreements with a hemiboreal Alno (incanae) -Fraxinetum (Kielland-Lund 1971). Oberdorfer (loc.cit.) has placed the plant community into Alnion glutinoso-incanae, in Doing (1962) Circae-Alnion, corresponding to Filipendulo-Fraxinion excelsioris (Passarge & Hofmann op.cit.) belonging to Alno - Fraxineta excelsioris (syn. Fagetalia sylvaticae) and Geranio-Fraxineta excelsioris (syn. Querco-Fagetea) including all rich deciduous forests (see Passarge & Hofmann op.cit., Westhoff & Den Held op.cit.).

Birch heath and birch fen vegetation

Myrico- Betuletum pubescentis (Osvold 1923) ass.nov. (Table XVII, distribution map 30)

Classification: Myrica gale, Dicranum undulatum and Pleurozium schreberi are differential taxa of Myrico- Betuletum pubescentis. Betula verrucosa belongs to a Betula verrucosa variant, Vaccinium vitis-idaea and Hylocomium splendens to a Vaccinium vitis-idaea variant. Betula pubescens is of high order and ranked with Pleurozio- Betulion pubescentis, Molinio- Betuleta pubescentis and Molinio- Betuletea pubescentis. The companion taxa are few, Aulacomnium palustre and Erica tetralix from Oxycocco-Sphagnetum, the graminids Carex nigra and C. arenaria and certain bryophytes.

Structure: The vegetation consists of an open to dense double or triple-layered plant community. Betula pubescens is the most prominent phanerophyte in some places as in coastal stands

with Betula verrucosa as a subdominant. Also coniferous trees may be present (see Fischer 1967 Table 4). The undergrowth is marked mainly with a rather homogenous layer of Myrica gale, as a rule the only nano-phanerophyte, more seldom scattered Rhamnus frangula. A field layer of the same height as Myrica gale or just below can be developed (see Almquist 1929 p. 319, Fischer loc.cit.) with various graminids as Molinia coerulea, often a dominant, Calamagrostis canescens and Carex spp., or be absent or nearly so (see Osvold 1923 p. 56). The ground layer is composed largely of pleurocarpic mosses such as Hylocomium splendens effectively covering the soil. In the moss carpet low-growing Erica tetralix and Vaccinium vitis-idaea are seen.

Development: Myrico- Betuletum pubescentis occurs in poor terrain depressions and on the margins of lakes and mires on sandy, rather acid soils with a high water table. Compared with other birch forests belonging to Molinio- Betuletea pubescentis the present plant community grows on drier habitats chiefly on mineral soil or drained mires with no longer any peat formation. According to Doing (1962 p. 68) Betula pubescens forests, poor in species and physiognomically unlike true deciduous forests must be regarded instable stages in the western coniferous-free area of Europe. They cannot be brought together in a unit of higher rank (Doing 1963 b) as proposed by Passarge & Hofmann (1968). The present abundance of certain birch forests is also the consequence of the destruction of stands with oaks, pines and spruces. Myrico- Betuletum pubescentis is often replaced by Vaccinio- Pinetum sylvestris and preceded by Molinio- Myricetum gale (see Malmer et al. 1965 p. 130) and is regarded a stage of the hygrosera, the oligotrophic subsere. Contacts with Caricetum canescentis-nigrae as well as with Agrostis tenuis - Populus tremula comm. occur.

Ecological remarks: The ecosystem is bound to mesotrophic habitats. The soil type is a hydromorphous soil or a wet podsol. In an analyzed stand the humus content at 0-5 cm is 13 %.

Distribution: Myrico- Betuletum pubescentis extends in the boreo-Atlantic and sub-Atlantic parts of Europe (Warming 1916-19 p. 491, Osvold loc.cit., Almquist loc.cit., Tüxen 1937 p. 126, Meijer Drees 1936 Table III, Sissingh 1941, Doing 1962, 1963 a, 1963 b, Fischer loc.cit., Passarge & Hofmann op.cit., Westhoff & Den Held 1969, Runge 1973).

The plant community occurs from Haverdal to Ängelholm, at Skanör's Ljung on the peninsula of Falsterbo (see Rasmusson & Rasmusson 1970) and as very small fragments at Sandhammaren and Revingehed.

Sociological relationships: Betuletum pubescentis (Tüxen loc.cit., Westhoff & Den Held op.cit.), Periclymeno-Betuletum (Scamoni & Passarge 1959 in Doing 1962) and Vaccinio-Betuletum pubescentis (Oberdorfer et al. 1967) are related to Myrico-Betuletum pubescentis. Betulion pubescentis has been placed into Vaccinietea uliginosi (Lohmeyer & Tüxen 1955 in Tüxen 1955), Sphagno-Betulion into Querco-Piceetea (Doing 1962). Westhoff & Den Held (op.cit.) has arranged Betulion pubescentis into Vaccinio-Piceetea (Braun-Blanquet et al. 1939). Passarge & Hofmann (op.cit.) have combined poor birch forests on mires and mineral soils into a specific class, Molinio-Betuletea pubescentis, with two orders Eriophoro-Betuletalia pubescentis and Molinio-Betuletalia pubescentis. The latter one includes Sphagno-Betulion pubescentis and Pleurozio-Betulion pubescentis to which Myrico-Betuletum pubescentis belongs.

Polytricho-Betuletum pubescentis (Osvald 1923) ass.nov. (Table XVII, distribution map 31)

Classification: Polytrichum commune, Sphagnum squarrosum and S. fimbriatum are differential taxa of Polytricho-Betuletum pubescentis. Carex nigra as a dominant forms a Carex nigra variant. Eriophorum angustifolium, Sphagnum recurvum and Carex rostrata constitute an Eriophorum angustifolium variant. Betula pubescens is of high order and ranked with Sphagno-Betulion pubescentis, Molinio-Betuletalia pubescentis and Molinio-Betuletea pubescentis. Quercus robur juv., Calamagrostis epigeios, Pohlia nutans and Aulacomnium palustre are among the few companion taxa.

Structure: The vegetation consists of an open to dense, double or triple-layered plant community. Often Betula pubescens is the only phanerophyte, low to high-growing. According to Malmström (1937 p. 402) other trees as Alnus glutinosa, sometimes a subdominant, Quercus sp., Sorbus aucuparia and Fagus sylvatica may be present. The birches are concentrated in the driest places, normally small hummocks. The birch regeneration is good as the many young individuals show. The nano-

phanerophytes, mainly Rhamnus frangula and Salix aurita, are nearly absent. However the researches of Libbert (1933 Table 30) and Passarge & Hofmann (1968 Table 34) show a tall shrub layer of structural importance. Various dwarf shrubs such as Vaccinium spp., prominent constituents in the inland forests (see Osvald 1923, Malmström loc.cit.), are absent or reduced in the coastal stands (see Hueck 1932 p. 121, Fukarek 1961 Table 43). At Sandhammaren in the analyzed stands also Molinia coerula is lacking, different from the conditions on the South Baltic coast (see Piotrowska 1955, Fukarek loc.cit.). The ground layer is irregularly developed often with Polytrichum commune growing in tufts of large hummocks, scattered with Aulacomnium palustre, surrounded by lower parts with Sphagnum spp. (see Malmström loc.cit.). In degenerated forests with dead birches, as in certain dune depressions, Carex nigra is very abundant and the bryophytes are reduced.

Development: Polytricho-Betuletum pubescentis forms instable fragmentary stands in wetland areas, edging mires or colonizing terrain depressions on the moraines or sandy fields, in weakly peaty soils on a mineral ground. The wooded bogs with Betula pubescens in the western and Pinus sylvestris in the eastern parts of Scania (see Malmer 1965 p. 151) are quite different stable plant communities referred to Eriophoro-Betuletalia pubescentis (Passarge & Hofmann loc.cit.). The hygrosera, the oligotrophic subsera, at Sandhammaren shows a regression to Caricetum canescentis-nigrae if the water table is too high or a succession towards Melampyro-Quercetum roboris if the water table is lowered. Carex nigra - Calamagrostis epigeios comm. is a transitional stage, Carex rostrata - Juncus effusus comm. and a Salix aurita tall shrub comm. are contact vegetation.

Ecological remarks: The ecosystem is bound to poor, acid minerotrophic habitats, normally with a fen peat soil or fen anmoor soil (see Duchafour 1970 p. 159) as at Sandhammaren. The brownish anmoor, varying from a few cm to about 20 cm, is irregularly decomposed lying directly on the sand. At 0-10 cm the humus content is about 9 %. A Betuletum pubescentis described by Fukarek (loc.cit.) has a peat layer of about 1 m and with a more acid soil reaction, in the surface soil 3.7 (in KCl 3.3) compared with 4.2 (3.5) at Sandhammaren, at 40-50 cm 5.2 (4.6).

Distribution: Polytricho- Betuletum pubescentis is scattered in the Eurosibiric region, in the western parts without pines (Osvald op.cit., Malmström loc.cit., Barkmann & Westhoff 1969 p. 358, Runge 1973) corresponding to the Erica-Regionale (Passarge & Hofmann 1968 p. 195), in the middle and eastern parts often with pines and Ledum palustre (Hueck loc.cit., Libbert loc.cit., Tüxen 1937 p. 127, Braun-Blanquet et al. 1939 pp. 68-70, Piotrowska 1955, Schubert 1960 Table 9, Fukarek loc.cit., Matuszkiewicz 1963, Passarge & Hofmann loc.cit., Passarge & Passarge 1972 Table 12) corresponding to a Ledum-Regionale (Passarge & Hofmann loc.cit.) sometimes transformed into a Ledo-Pinetum (Syn. Vaccinio uliginosi - Pinetum sylvestris) as can be seen in Matuszkiewicz (op.cit.), Wojterski (1963) and Malmer (loc.cit.). A southern submontane vicariant with Holcus mollis is reported by Büker (1942) and Oberdorfer (1957). Within the investigation area Polytricho- Betuletum pubescentis is found only at Sandhammaren.

Sociological relationships: Hueck (loc.cit.), Libbert (loc.cit.) and Tüxen (loc.cit.) have analyzed different Betuletum pubescentis. Tüxen (1955) has separated a Pineto- Ledetum sylvestris belonging to a Pino- Ledion palustris from Betuletum pubescentis. Matuszkiewicz (op.cit.) has studied the geographical difference between Betuletum pubescentis and Vaccinio uliginosi -Pinetum. Passarge & Hofmann (loc.cit.) have introduced a Sphagno- Betuletum pubescentis belonging to Sphagno- Betulion pubescentis (Doing 1962). The floristic structure with the presence of Eriophorum vaginatum is different from the proposed Polytricho- Betuletum pubescentis and probably has stronger agreements with a Polytricho-Betuletum (boreale) of the boreal vicariant class Vaccinio- Betuletea pubescentis (Passarge & Passarge op.cit.) than to Molinio-Betuletea pubescentis.

Sandy wetland vegetation

Low vegetation

Carex nigra - *Calamagrostis epigeios* community, prov., (Table XVIII, distribution map 32)

Classification: *Calamagrostis epigeios* is a local differential dominant of a *Carex nigra* - *Calamagrostis epigeios* community. *Carex nigra* and

certain plants from Deschampsio- Quercetea robori-petraeae are among the companion taxa.

Structure: The vegetation consists of a single-layered plant community physiognomically determined by the luxuriance of *Calamagrostis epigeios* and scattered *Carex nigra*.

Development: Isolated clones of *Calamagrostis epigeios* are normally associated with extremely dry places such as clearings, forming a *Calamagrostidetum epigeios* (Juraszek 1928, Regel 1928, 1944, Runge 1973). According to Almquist (1929 p. 239) a 'Calamagrostis epigeios -hed' is common along the coast though fragmentary as seen at Ängelholm and Tönnersa. On sandy lake shores or along rivers, e.g., the river Tygeån at Sandhammaren, *Calamagrostis epigeios* can colonize, but not in pure stands, forming a margin community related to an *Eupatorium cannabini Calamagrostis epigeios* sub-ass. (Krausch 1970 Table 11). In dune depressions *Calamagrostis epigeios* is a pioneer, often together with *Salix arenaria*, under specific circumstances also without (Paul 1944 pp. 328-337, Steffen 1931 p. 276). The present plant community seems to be a gradient stage between Polytricho- Betuletum pubescentis and Melampyro- Quercetum roboris on wetter and drier ground respectively.

Ecological remarks: The ecosystem is confined to wet, very instable sandy habitats.

Distribution: A *Carex nigra* - *Calamagrostis epigeios* comm. seems to occur fragmentarily in certain Baltic dune depressions (Steffen loc.cit., Paul loc.cit.), within the investigation area only at Sandhammaren.

Sociological relationships: It is very difficult to place a *Carex nigra* - *Calamagrostis epigeios* comm. into a phytosociological system, since there are no agreements with *Epilobietea angustifolii* (see Runge loc.cit.) on instable dry places or with *Artemisietea vulgaris* (see Krausch loc.cit.) in a more stable gradient milieu. Relationships with *Melampyro-Quercetum roboris* and with Polytricho- Betuletum pubescentis are also found.

Carex rostrata - *Juncus effusus* community comm.nov. (Table XVIII, distribution map 33)

Classification: *Carex rostrata* and *Juncus effusus* constitute a local characteristic combination. A *Carex rostrata* sociation as well as a *Carex nigra* variant with *Carex nigra*, *Betula pubescens* juv. and



Fig. 17. *Carex rostrata* - *Juncus effusus* comm. with dead birches. Sandhammaren 1971. Photo H. Olsson.

Pohlia nutans are distinguished. *Alnus glutinosa* juv. and *Calamagrostis epigeios* are the most prominent companion taxa.

Structure: The vegetation consists of a dense, single-layered gradient plant community dominated by *Juncus effusus* on drier and *Carex rostrata* on wetter habitats. In intermediate stands *Carex nigra*, *Calamagrostis epigeios* and *Alnus glutinosa* juv. have certain structural importance.

Development: A *Carex rostrata* - *Juncus effusus* gradient comm. seems to occur in certain terrain depressions, bordering on drained mires and in wetland grazing areas. With human influence, *Juncetum effusi* (Vallin 1925 p. 32, Jonas 1935, Westhoff & Den Held 1969 p. 115) with *Hydrocotyle vulgaris* and sometimes with a moss layer with *Sphagnum* spp. and *Drepanocladus fluitans* is developed in a similar way in poor/rich minerotrophic gradient habitats. *Carex rostrata* stands in rather uninfluenced mires contain only little *Juncus effusus* (see Osvald 1923 p. 168). At Sandhammaren in the outer dune depressions the gradient community has developed in a natural way due to fluctuations in the water table sharply bordered by surrounded vegetation, as *Caricetum canescentis -nigrae* or degenerated *Polytrichum-Betuletum pubescentis*.

Ecological remarks: The ecosystem is characterized

by wet habitats. On the ground there is usually water during a long period of the year. The soil type is a fen anmoor soil or a fen peat soil, at Sandhammaren probably both. The humus layer is highly decomposed, lying directly on the sand. In the surface soil the humus content is about 35 %. The pH is 4.9 (in KCl 3.9).

Distribution: Very little is known about the range of a *Carex rostrata* - *Juncus effusus* comm. (see Vallin loc.cit., Jonas loc.cit., Osvald loc.cit., Passarge 1964 a p. 216, Ratcliffe 1964 Table 56); within the investigation area only at Sandhammaren.

Sociological relationships: According to Westhoff & Den Held (1969 p. 107) *Carex rostrata* - *Juncus effusus* comm. has been placed into *Agropyro-Rumicion crispae*, especially the suballiance *Juncion effusi* representing plant communities in a poor/rich gradient, belonging to *Plantaginietalia majoris* and *Plantaginetea majoris*.

Caricetum canescentis -nigrae (Br.-Bl. 1915) Vlieger 1937 (sub nom. *Caricetum canescentis -fuscae*) (Table XIX, distribution map 34)

Classification: *Carex canescens* and *C. echinata* are characteristic taxa of *Caricetum canescentis -nigrae*. A *Carex canescens* sociation as well as a *Sphagnum recurvum* subass. are registered. *Sphagnum recurvum*, *Drepanocladus fluitans*, *Polytrichum commune*, *Calliergon stramineum* and *Calypogeia sphagnicola* are differential taxa of the latter one, in which a *Calamagrostis canescens* variant with *Calamagrostis canescens*, *Naumburgia thyrsiflora* and *Iris pseudacorus* is separated. *Carex nigra* and *Juncus filiformis* belong to *Caricion canescentis -nigrae*. *Eriophorum angustifolium*, *Potentilla palustris*, *Calliergon cordifolium*, *Drepanocladus exannulatus* and *Riccardia pinguis* are of high order and ranked with *Caricetalia nigrae* and *Parvocaricetea*. Plants from *Molinio-Arrhenatheretea* such as *Juncus conglomeratus*, *Lysimachia vulgaris*, *Galium uliginosum* and *Lythrum salicaria* are among the companion taxa as well as *Juncus effusus*, *Salix aurita* and *Myrica gale*.

Structure: The vegetation consists of an open to closed, double-layered plant community dominated by graminids and *Sphagnum* spp. The homogenousness is reduced due to the variation in number of species, frequency and degree of cover (see Larsson, A. & Svensson 1972 Table 4).

Although the structural constituents of *Caricetum canescentis -nigrae* from certain coastal dune depressions (see Wangerin 1921 pp. 372-376, Fukarek 1961 Table 43) are nearly the same as in inland poor fen vegetation (see Malmer 1965 p. 153), the physiognomy is often determined by only one species. Various inland stands contain *Carex rostrata* (see Waldheim & Weimarck 1943, Nordborg & Nordborg 1957, Malmer 1962, Svensson 1965) in contrast to several maritime stands. The *Carex canescens* soc. is recognized by grassy tufts and by scattered dead birches. *Carex canescens* is also found together with *Eriophorum angustifolium* in hollows with *Sphagnum recurvum* and *Drepanocladus fluitans*. *Calamagrostis canescens* may be predominant in fens often influenced by man (Osvald 1923 pp. 146, 188, Krausch 1968 p. 324). In the present variant *Juncus filiformis* is an important component sometimes less common in the inland.

Development: On water-logged soil in mire margins a poor fen, *Caricetum canescentis-nigrae*, is developed in mesotrophic or oligotrophic habitats. Anthropogenously substituted communities, carr forests on poor stands, form transitional fens (see Waldheim & Weimarck op.cit.), often situated along periodically inundated lake shores (see Larsson, A. & Svensson op.cit.) and rivers (see Rühling 1968). A water-logged soil is also typical of the dune depressions, with fragments of unstable poor fens, according to Westhoff (1947 p. 111) transformed into a *Myricetum gale* probably corresponding to *Molinio-Myricetum gale Salix arenaria* subass. but in the hygrosere, the oligotrophic subsere, also directly to *Myrico-Betuletum pubescentis* or *Polytricho-Betuletum pubescentis*. *Caricetum acutae*, *Carex rostrata - Juncus effusus* comm., and plant communities from *Carici-Salicetea cinerea* are often in contact.

Ecological remarks: The ecosystem is bound to minerotrophic milieus poor in nutritive substances. The soil type is a fen anmoor soil or a fen peat soil, in the dune depressions mainly the former. At Tönnersa a thin brownish humus layer, often only 5 cm, lies directly on the sand. At 0-10 cm the organic matter is only about 6 %. The average pH is 5.1 (in KCl 4.3).

Distribution: *Caricetum canescentis -nigrae* occurs in large parts of the Eurosibiric region, mainly in the

boreal montane area, as well as in the Atlantic or sub-Atlantic parts (Wangerin loc.cit., Jonas 1933, 1935, Tüxen 1937 pp. 62-63, Braun-Blanquet & Tüxen 1952, Oberdorfer 1957 p. 165, Neuhäusel 1959, Fukarek op.cit., Jeschke 1963 Table 24, Passarge 1964 a pp. 215-216, Horst et al. 1966 Table 15, Krausch 1968 b Table 1, Westhoff & Den Held 1969 pp. 199-200). The following works from Middle and South Sweden may be mentioned: Osvald loc.cit., Waldheim & Weimarck 1943, Sjörs 1948, Nordborg & Nordborg op.cit., Malmer 1962, 1965, Svensson 1965, Rühling 1968, Andersson, L. 1971 Table 4, Larsson, A. & Svensson loc.cit. A coastal *Caricetum trinervis -nigrae* is regarded a vicariant (Westhoff loc.cit., Westhoff & Den Held loc.cit.). Within the investigation area *Caricetum canescentis -nigrae* has been found at Haverdal, Tönnersa and Sandhammaren, at the two first localities only *Sphagnum recurvum* subass. *Calamagrostis* var., at Sandhammaren both *Sphagnum recurvum* subass. and a *Carex canescens* soc.

Sociological relationships: Tüxen (loc.cit.) has proposed a *Caricetum canescentis - Agrostidetum caninae* from which Krausch (1968 b) has separated a *Sphagnum recurvum* subass. having agreements with the present plant community. *Caricion canescentis -nigrae* (syn. *Caricion curto -nigrae* Westhoff & Den Held loc.cit.) have been investigated by several authors (Koch 1926, Nordhagen 1936, Tüxen 1937 see in Westhoff & Den Held loc.cit.). In the system of Westhoff & Den Held (loc.cit.) *Caricetalia nigrae* is placed into a *Parvocaricetea*, syn. *Vaginato-Sphagnetes* prov. (Malmer 1968 a).

Marsh vegetation

Caricetum acutae (Almquist 1929) R.Tx. 1937 (sub nom. *Caricetum gracilis*) (Table XX, distribution map 35)

Classification: *Carex acuta* is a characteristic taxon of *Caricetum acutae*. *Polygonum amphibium* is a differential taxon of a *Polygonum amphibium* subass. *Campylium polygamum*, *Galium uliginosum* and *Calliergon cordifolium* belong to a *Campylium polygamum* subass. *Galium palustre*, *Scutellaria galericulata*, *Naumburgia thyrsiflora* and *Carex acutiformis* are among *Magnocaricion* and *Magnocaricetalia*. *Iris pseudacorus*, *Phragmites communis*, *Peucedanum palustre*, *Lycopus*

Fig. 18. *Caricetum acutae*, in the foreground *Molinio-Myricetum gale Salix arenaria subass.*, in the background *Alno-Salicetum cinereae*. Tönnersa 1971. Photo H. Olsson.



europaeus and *Alisma plantago-aquatica* are ranked with *Phragmitetea*. The companion taxa are chiefly from *Molinio-Arrhenatheretea*, such as *Lythrum salicaria* and *Lysimachia vulgaris*, and from *Parvocaricetea*, such as *Potentilla palustris* and *Carex nigra*. Furthermore there is *Salix cinerea*.

Structure: The vegetation consists of a closed to very closed plant community of high-growing graminids in general totally dominated by *Carex acuta*. The vegetation is single-layered in *Polygonum amphibium subass.* characteristic of *Phragmitetea*. The high degree of homogeneity is a consequence of the floristic situation with few plants (see Almquist 1929 Table 12, Nordborg & Nordborg 1957, Mörnjö 1969 Table 2, Larsson, A. 1971, Andersson, L. 1971 Table 6). Mörnjö (loc.cit.) has estimated the density of the dominant *Carex acuta* to 400-500 shoots/m², 90-120 cm in length. In an adjacent grazed area the shoot density is more variable and the shoot length only 50-60 cm. The length amplitude in the coastal stands is about 50-100 cm. Andersson, L. (loc.cit.) has reported an inland stand with a larger quantity of herbs, only rarely with *Polygonum amphibium*, *Lythrum salicaria* and *Potentilla palustris* in the coastal ones. In the *Campylium polygamum subass.* the tendency of two layers is obvious, which is shown by the presence of *Calliargon cordifolium*, *Campylium polygamum* and *Drepanocladus exannulatus* (see Blažková 1971 Tables 1-2). The homogeneity has decreased somewhat and the number of plants have increased, especially the density of *Phragmites communis* and

Carex nigra in one stand as well as *Peucedanum palustre* and *Lysimachia vulgaris* in a second one. As a whole *Caricetum acutae* on the Continent are richer in species (Passarge 1964 a, Konczak 1968, Blažková loc.cit.) than in South Sweden.

Development: On wet alluvial soils in inundated eutrophic habitats along shore lakes and rivers and certain terrain depressions in the wetland a semi-aquatic marsh community, *Caricetum acutae*, may be developed. The water table may be strongly changed during the year. It is normally below the superficial parts only in the summer months. The plant community may be a substitute of *Irido-Alnetum glutinosae* but more often of natural primary origin, in the hygrosere, the eutrophic sub-sere. An *Alno-Salicetum cinereae* is often in contact as well as *Caricetum canescentis-nigrae* and various aquatic plant communities, e.g., *Sparganium minimum comm.*

Ecological remarks: The ecosystem is characterized by minerotrophic habitats rich in nutritive substances. The humus is built up both allochthonously via supplied sediments from the inundated water, and autochthonously by a rapid humification of decomposed organic matter. The soil type is an *aeu* soil or *anmoor fen* soil. In *Polygonum amphibium subass.* the humus layer is about 10 cm, tough, black, highly decomposed, sharply bordering on the mineral soil. In *Campylium polygamum subass.* the layer is smaller and the humus more irregularly decomposed. The humus content is nearly 30 % at 0-10 cm in the first subass., only about 4 % in the se-

cond. The corresponding pH is 4.9 (in KCl 4.4) and 5.6 (4.5) respectively. The present figures are very low, in Konczak (loc.cit.) 5.5-6.6, in Géhu (1961 p. 121) 6.5-8.0.

Distribution: *Caricetum acutae* occurs in the lowlands, more rarely in the highlands in large parts of Europe (Jonas 1933, Hueck 1934, Tüxen 1937, Oberdorfer 1957, Neuhäusl 1959, Géhu loc.cit., Passarge 1964 a, Balátová-Tuláčková 1963, Horst et al. 1966, Konczak loc.cit., Westhoff & Den Held 1969 p. 143, Blažková loc.cit., Runge 1973), including South and Middle Sweden (Almquist loc.cit., Nordborg & Nordborg op.cit., Rühling 1968, Mörsjö loc.cit., Andersson, L. loc.cit., Larsson, A. loc.cit.). *Caricetum acutae* is found at Tönnersa and Haverdal, *Polygonum amphibium* subass. on both and *Campyllum polygamum* subass. only on the first locality.

Sociological relationships: Almquist (loc.cit.) has proposed a naked *Carex gracilis* ass. modified by Tüxen (op.cit.) to *Caricetum gracilis* with a rank in the Braun-Blanquet system. Several aspects of a separation of *Caricetum acutae* are given. Passarge (1955 see 1964 a) has introduced a typical sub-association and a comaretosum, Konczak (loc.cit.) a *Comarum palustre* subass. and a *Ranunculus repens* subass., Blažková (loc.cit.) a typical subassociation, comaretosum and naumburgietosum, all having certain agreements with the present *Polygonum amphibium* subass. The second *Campyllum polygamum* subass. may be confined to the coast. Koch (1926) has pointed out a *Magnocaricion elatae*, in Westhoff & Den Held (loc.cit.) only *Magnocaricion*. Balátová-Tuláčková (op.cit.) has separated two alliances, *Caricion gracilis* and *Caricion rostratae*, according to Oberdorfer et al. (1967) only suballiances. Passarge (1964 a) has used *Magnocaricion elatae* and (Magno-) *Caricion gracilis* (Neuhäusl 1959, Géhu loc.cit.). Westhoff & Den Held (loc.cit.) and Oberdorfer et al. (op.cit.) have placed only one alliance into *Magnocaricetalea* belonging to *Phragmitetea*.

Aquatic vegetation

Sparganium minimum community Westhoff 1968 (Table XX, distribution map 36)

Classification: *Sparganium minimum* is a local

characteristic and as a rule dominant taxon of a *Sparganium minimum* community. *Polygonum amphibium* and *Alisma plantago-aquatica* are among the companion taxa.

Structure: The vegetation consists of a very closed, single-layered plant community dominated by the small nymphaids, *Sparganium minimum*, with the green slender leaves totally covering the surface of water. Other plants are scattered or occasional. In a related community in the mire districts *Utricularia* spp. are closely associated (see Osvald 1923 p. 242, Tüxen 1937 p. 45, Müller & Görs 1960 Table 4).

Development: A *Sparganium minimum* comm. occurs rarely in small pools with stagnant or weakly flowing water with a water depth of 10-50 cm. If the water in the summer months dries up, *Sparganium minimum* can change from aquatic to terrestrial growth (Krausch 1968 b p. 343). The plant community can be in contact with aquatic or semi-aquatic communities such as *Caricetum acutae*.

Ecological remarks: The ecosystem according to Westhoff & Den Held (1969 p. 59) has its optimum in a mesotrophic milieu, as in the dune depression at Ängelholm. A *Sparganietum minimi* (see Müller & Görs loc.cit.) has its optimum in an oligotrophic milieu.

Distribution: According to Müller & Görs (loc.cit.) *Sparganietum minimi* has about the same range as *Sparganium minimum* in the boreal-sub-Oceanic area (Tüxen 1937 p. 45, Osvald loc.cit., Oberdorfer 1957, Neuhäusl 1959, Müller & Görs loc.cit., Jeschke 1963, Krausch loc.cit., Passarge 1964 a, Runge 1973); the *Sparganium minimum* comm. (Hartog & Segal 1964 p. 389, Westhoff & Den Held loc.cit.) within the investigation area at Ängelholm.

Sociological relationships: Müller & Görs (loc.cit.) have placed *Sparganietum minimi* (Schaaf 1925, Tüxen 1937 see Müller & Görs loc.cit.) into *Sphagno-Utricularion* belonging to *Littorelletea*. *Sparganium minimum* comm. has been classified under *Potamion graminei* belonging to *Luronio-Potametalia* and *Potametea* (Den Hartog & Segal 1964, Westhoff & Den Held loc.cit.).

Vegetational changes and soil development

THE HALO-NITROSERE

In the sense of Westhoff (1947) the halosere comprises vegetation of the intertidal zone, succession stages initiating on silt or silty sandy soil regularly inundated by the sea. In Sweden the halosere is confined mainly to the outer zones of the seashore meadows (Dahlbeck 1945, Gillner 1960, Tyler 1969). The nitrosere is proposed to include vegetation, not directly maritime-influenced, of various gradient milieus and often with ruderal communities belonging mainly to *Chenopodietea*, *Artemisietea vulgaris* and *Plantaginetea majoris*, as well as the nano-phanerophyte class *Urtico-Sambucetea*. Westhoff (op.cit.) has separated two series 'halosere on mud' and 'halosere on sand', the latter one having agreements with the present halo-nitrosere with irregular inundations and fluctuations of the salt content parallel to a humus accumulation of drift material.

As seen in Fig. 19 the halo-nitrosere is divided into two series: in the first one there are communities of *Cakiletea maritima* developed into *Agropyro-Rumicion*, in the second series there is a perennial drift vegetation, mainly of *Agropyretea pungentis*. The first part of the sere is started with *Cakiletum maritima* and continued with *Atriplicetum littoralis* both rich in therophytes. In stable habitats appear *Agropyro-Rumicion crispis* with many hemi-cryptophytes. Here the halophilic tendency has decreased. Instead the nitrophilic milieu is obvious, often on places inside stony sandy shores with old accumulated drift material. Dahl & Hadač (1941 p. 303) have coupled the halosere with the halo-nitrosere. In the latter one an *Atriplicetum littoralis* is developed into an *Elymetum arenarii*, related to

Potentillo-Elymetum (Tüxen 1966), as well as into an *Euphorbietum palustris*. The soil type is a beach syrosem with an increased drift layer with a neutral soil reaction.

Degenerated *Cakiletum maritima*, especially *Cakile maritima* soc., may be a base of *Honkenyetum peploidis* initiating a second series of halo-nitrophilic vegetation in instable habitats on seashores with sand, gravels or stones on offshore barrier islands (see Gravesen & Vestergaard 1969), on coasts with marine accumulation (see Böcher 1952 b) or semi-protected, as near Vegeholm on the bay of Skälderviken. Warming (1906 pp. 53-58) and Böcher (op.cit.) have given a more comprehensive picture of the changes of *Honkenyo-Crambetalia maritima* including a development from *Honkenyetum peploidis* via *Crambetum maritima* to a *Beta maritima* comm. not registered in South Sweden, where at Falsterbo *Honkenyo-Agropyretum acuti* and *Lepidietum latifolii*, both belonging to *Agropyretalia pungentis*, are succeeded by *Honkenyetum peploidis*. In *Honkenyo-Agropyretum acuti* the halo-nitrophilic tendency is recognized by the luxuriant *Elymus arenarius*, on the small island of Måkläppen also guanotrophically influenced. In the oligohalinic zone *Lepidietum latifolii* seems to be transformed into *Agropyro-Rosetum rugosae*. Stability and salinity are more important factors than changes in organic matter. The soil type is a syrosem mixed with tang with rather small changes. The soil reaction is about neutral.

THE XEROSERE

The maritime dune subsere

The xerosere has been divided into the maritime

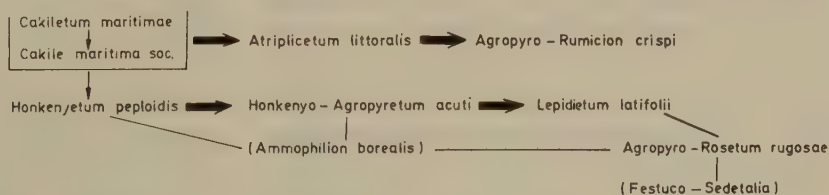


Fig. 19. The halo-nitrosere.

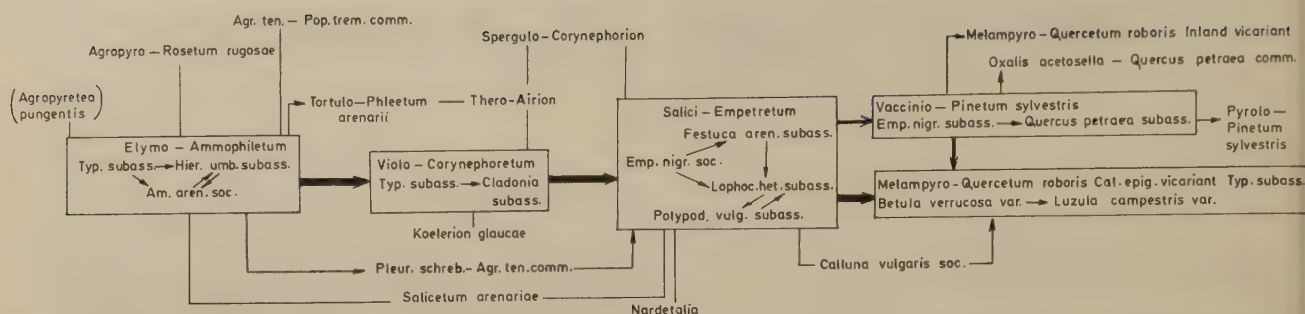


Fig. 20. The xerosere, the maritime dune subseres.

dune subseres, the subseres comprising sands affected by man and the glaciifluvial subseres. The first one as seen in Fig. 20 corresponds to a distinct succession on maritime sands, from the pioneer vegetation on embryo dunes to a climax community, a steady state forest (Tomuschat & Ziegenspeck 1929, Fukarek 1961, Ellenberg 1963, Chapman 1964, Géhu 1964, Tüxen 1967 c). Whittaker (1953) says that common to succession and the climax is the interplay of populations, which in succession is expressed in directional change and in the climax as fluctuation around an average. Similar or convergent community patterns tend to develop in adaptation to similar environments. Change in environment implies change in the community pattern.

The present vegetational succession starts with Elymo-Ammophiletum, continues with Violo-Corynephoretum, and Salici-Empetretum and reaches a climax, not prevailing but rather split, of Melampyro-Quercetum roboris Calamagrostis epigeios vicariant (Sandhammaren), inland vicariant (Ängelholm), Oxalis acetosella - Quercus petraea comm. (Haverdal) and Pyrolo-Pinetum sylvestris (Furuboda). In the Atlantic region the final stage is regarded an oak forest (Chapman op.cit., Géhu op.cit., Tüxen op.cit.), along the Swedish coast obviously seen in the province of Bohuslän (Tüxen 1951, Ivarsson 1962, Ivarsson & Hallberg 1965), at Sandhammaren (Olsson 1972 a) and probably in coastal parts of the province of Blekinge (Berglund 1963) as well as on the small island Blå Jungfrun (Ottoson 1965) in the province of Småland. On the bay Hanöbukten at Furuboda there is probably a Pyrolo-Pinetum sylvestris, although an old oak forest close to Espet near the small village of Åhus is found, and thus it partly agrees with the climax situation on the opposite Baltic side where a coniferous forest is prevalent (Wojterski 1964 a). Vaccinio-Pinetum sylvestris Empetrum nigrum subass. in

South Sweden is regarded only a subclimax and is continuously transformed into a more stable condition as represented by the four above-mentioned plant communities.

Elymo-Ammophiletum, in some places initiating from destroyed Agropyrea pungentis, is developed in the geo- and epilittoral zone on the dunes, where variations in sand accretion may lead to a cyclic process manifested by Ammophila arenaria soc. This process comprises 'Die Kampfkomplexe' (Regel 1928), an association complex on moving loose sand, in which Agropyro-Rosetum rugosae has fortified its position and Salicetum arenariae constitutes another cyclic phenomenon. With normal ageing of the dunes Elymo-Ammophiletum disappears as a consequence of reduction or cessation of sand accretion, also indirectly affected by replanted Ammophila arenaria (Jansson 1959, Hewett 1970). Violo-Corynephoretum is established on the same level as Elymo-Ammophiletum Hieracium umbellatum ssp. subass. and favoured by an instable sand or moderate sand burial. The development, only partly corresponding to 'die Ruhekomplexe' (Regel op.cit.), may be complicated, as shown by van Dieren (1934 p. 202), as processes go on parallel to each other in various zones marked by accumulation, corrosion and deflation. Violo-Corynephoretum is succeeded by Salici-Empetretum. At Falsterbo a Tortulo-Phleetum arenarii is rarely a link between Elymo-Ammophiletum and Thero-Airion. The latter is possibly in contact with Spargulo-Corynephorion, rarely adjacent to Salici-Empetretum, which colonizes a Pleurozium schreberi - Agrostis tenuis comm. at Ängelholm replacing Elymo-Ammophiletum. At Vitemölla, furthermore, Violo-Corynephoretum borders on Koelerion glaucae. Moreover, Salici-Empetretum may be in contact with Spargulo-Corynephorion, Salicetum arenariae, Nardetalia and Calluna vulgaris soc. Of special in-

terest are the intrastructural changes. A very rapidly settled *Empetrum nigrum* soc. is transformed into a more stable *Lophocolea heterophylla* subass. or via another pioneer stage into *Festuca arenaria* subass. The changes seem to be both progressive and regressive where there is an interaction between *Violo-Corynephorum*, in some places also *Cladonio-Corynephorum*, and *Salici-Empetretum* (Böcher 1941 b, 1952 a). At Sandhammaren the reversible development between *Polypodium vulgare* subass. and *Lophocolea heterophylla* subass. is observed.

Salici-Empetretum Lophocolea heterophylla subass. is replaced by a forest, on the west coast a *Vaccinio- Pinetum sylvestris Empetrum nigrum* subass., at Haverdal succeeded by a *Quercus petraea* subass., at Sandhammaren by *Melampyro-Quercetum roboris Calamagrostis epigeios* vicariant. The last-mentioned is the primary stage, in many cases the only one, and initiated by a *Betula verrucosa* var. (see van der Maarel & Westhoff 1964 p. 10, van der Maarel 1966 p. 68) of short duration and developed into a *Luzula campestris* var. Plant communities in subclimax and climax comprise a part of 'Die Klimaxkomplexe' (Regel op.cit.).

In the xerosere maritime dune subere the soil undergoes a gradual change from dune syrosem, via ranker towards podsol or podsoloid (see Reuter 1957/58 p. 668). The syrosem skeleton is a well-sorted sand with an (A)-C-profile also showing elongated rhizomes and humus lenses, in *Elymo-Ammophiletum Hieracium umbellatum* spp. subass. with a syrosem-humus (cf. Kubišna 1953 p. 188). Between syrosem and ranker there is often a ranker-dune syrosem (see Mückenhausen 1962 p. 52) such as of *Violo-Corynephorum* and *Salici-Empetretum Festuca arenaria* subass. with a more pronounced humus layer, A, in the surface soil. The ranker is characterized by a raw humus on a sand with a humus mixture and marks later stages of *Salici-Empetretum*, where the litter fall has increased. A ranker is shown in Fig. 21. A development from a young syrosem to a podsol with pronounced eluvial and illuvial zones takes about 200 years (Fukarek 1961 p. 153). In *Vaccinio-Pinetum Quercus petraea* subass. the soil is younger and, below a thick litter and moss layer, the well-developed raw humus zone is replaced by a diffusely eluvial horizon above the B- and C-layers (see Table XXII). In *Melampyro-Quercetum roboris* Vac-

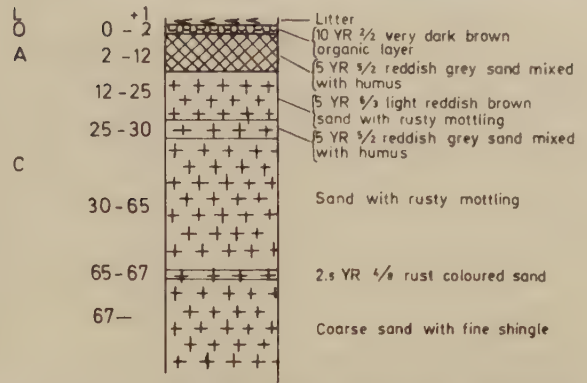


Fig. 21. Soil profile from *Salici-Empetretum Lophocolea heterophylla* subass. Haverdal (1972-5).

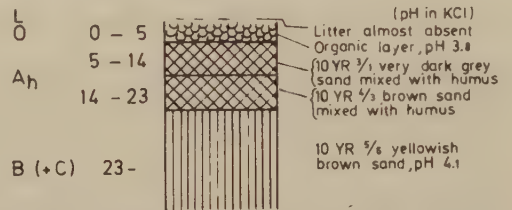


Fig. 22. Soil profile from *Oxalis acetosella - Quercus petraea* comm. Haverdal (1972-5).

cinium myrtillus var. and *Pteridium aquilinum* var. the soils are considered to be very old; in the first one the raw humus is about 15 cm and in the second one there is a pan at 50 cm (see Table XXII). Here the eluvial zones seems to be lacking, differing from the strong podsol described by Fukarek (loc.cit.) from Darss in the DDR and Piotrowska (1960) from the Polish island of Uznam. In the *Oxalis acetosella - Quercus petraea* comm. there is a podsoloid with a very diffuse soil stratification (Fig. 22).

Plant succession and soil development are controlled by the time factor (Olson, J. 1958, Wilson 1960) and a correlation with changes in soil pH and organic matter has been found. The soil reaction has become continuously stronger and the pH is lowered from 6.2 (in KCl 5.4) in the surface soil, 6.8 (6.0) in the subsoil, to 4.1 (3.1) and 4.6 (3.8) respectively in the development from dune syrosem to podsol; in the podsoloid the pH is somewhat higher as well as in the inland vicariant of *Melampyro-Quercetum roboris*. Parallel to the decrease in pH the organic content has increased from 0.20 % in the surface soil and 0.17 % in the subsoil to 10-50 % and ca. 1 % respectively.

The subere of the sands affected by man

Certain trends or progressive developments toward the climax may characterize another successional

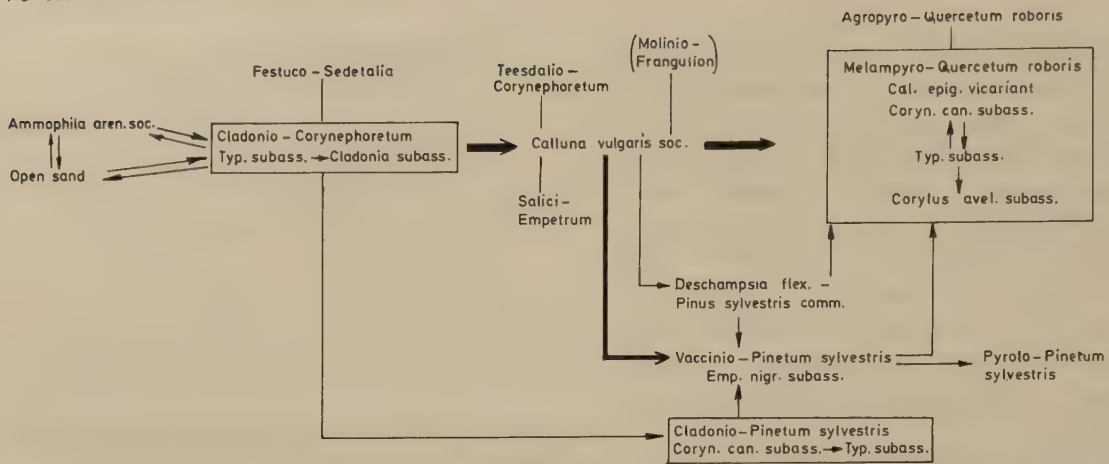


Fig. 23. The xerosere, the subsere of the sands affected by man.

evolution initiated by human influences, such as felling, burning and grazing, since the middle of the 17th century. According to Whittaker (op.cit.) there is a progressive increase in community complexity and diversity, stature and productivity, maturity of soil and relative stability, and regularity of populations often spread as clones around parent individuals. The present succession is started as a rule on eroded patches with *Cladonio-Corynephoretum*, also coupled to a cycle with *Ammophila arenaria* soc. and the naked sand (Fig. 23) and in some places in contact with *Festuco-Sedetalia*, replaced by a *Calluna vulgaris* soc. and in later stages by various forests in subclimax or climax. The process is a closing of earlier open dune landscape (see Söderlingh 1698, Kanter 1750, Dahlbom 1777/78, Lindblom 1782, Vistelius 1891, Wibeck 1906, Hesselman 1908, Tüxen 1928, Krieger 1937, Arwidsson 1938, Böcher 1941 a, Sjögren 1957, Troedsson 1964, Olsson et al. 1971, Arwidsson 1938).

The closing of the plant cover by *Ammophila arenaria* plantations continued in a slow tempo between 1700-1830 and then accelerated and today most fields are overgrown. At Haverdal (Kanter op.cit.) a main part of the sands was naked or occupied by heather, today only near the seaward dunes. At Sandhammaren the dwarf shrub heath has decreased from about 300 ha to 70 ha.

Calluna vulgaris soc. is at Revingehed in contact with *Teesdalia-Corynephoretum* related to a *Polytrichum piliferum* soc. (Böcher op.cit. Table 13), at Sandhammaren with *Salici-Empetretum* and *Molinio-Frangulion*. On the latter place it has developed into *Melampyro-Quercetum roboris* *Calamagrostis epigeios* vicariant or to a lesser extent

into *Vaccinio-Pinetum sylvestris* *Empetrum nigrum* subass., the latter of which is colonized by oaks. Otherwise, as at Ängelholm and Furuboda, the fragments of *Pyrolo-Pinetum sylvestris* are in climax. The afforestations mainly on the dwarf shrub heath have resulted in a *Deschampsia flexuosa* - *Pinus* comm., which may proceed into *Cladonio-Pinetum sylvestris* (originated from *Cladonio-Corynephoretum*). The latter *Pinetum* is also transformed into *Vaccinio-Pinetum* *Empetrum nigrum* subass. The main pathway to the oak forest is via oak regeneration in *Calluna vulgaris* soc. The oak has also the ability to supersede the pine in the coniferous forests, especially those with graminids and nano-chamaephytes. The diversity and stature of *Melampyro-Quercetum roboris* *Calamagrostis epigeios* vicariant, less common in contact with *Agrostio-Quercetum roboris*, undergoes intraspecific changes seen in the reversible development between a typical subassociation and a *Corynephorus canescens* subass. More rarely the former one is replaced by *Corylus avellana* subass. The oak bunches in the typical subassociation (Weimarck 1960, Olsson 1972 a) are a result of a clone grown up around a parent individual. Olsen (1938 Table 7) has studied a vegetation similar to the present typical subassociation and proposed a successional evolution from mesophytes, such as *Anthoxanthum odoratum*, to acidophytes, such as *Vaccinium myrtillus* and *Pteridium aquilinum*, parallel to the progressive process of increased raw humus formation in a series from podsoloid to podsol.

The interactions between the oak and the pine are a chief problem in this subsere. On old maps (Kanter

op.cit., Dahlbom 1777/78), illustrated in Figs. 32-36. the pine is nearly lacking, but today it is the most prevalent tree on the sands at Sandhammaren (ca. 270 ha), where, however, the oak trend is increasing; the same is also observed at Haverdal, Ängelholm, Hemmestorp and Vitaby. At Sandhammaren pollen-analysis has been performed to study changes in forest composition (Table XXI). *Calluna*-pollen has high figures in the oak subsoil and the pine surface soil, which is an indication of an afforested dwarf shrub heath. *Quercus*-pollen has high figures only in oak surface soil, in the subsoil replaced by *Betula* and *Alnus*. Pine-pollen has high figures in pine surface soil and deep pine subsoil. In the surface soil of a birch fen *Alnus*-pollen is more predominant than *Betula*-pollen. The production of *Alnus*-pollen is high and the presented figures may be misleading. As a whole the result of the pollen-analysis indicates difficulties in drawing conclusions concerning the vegetation history. From the opposite Baltic coast Paul (1944) and Fukarek (1961) have discussed the composition of an earlier forest, a mixed forest with pine, oak and various deciduous trees, where now *Pinus sylvestris* is in climax.

Cladonio-Corynephorum has formed a ranker-dune syrosem where the surface sand is mixed with humus to 10-20 cm. The soil development leads to a

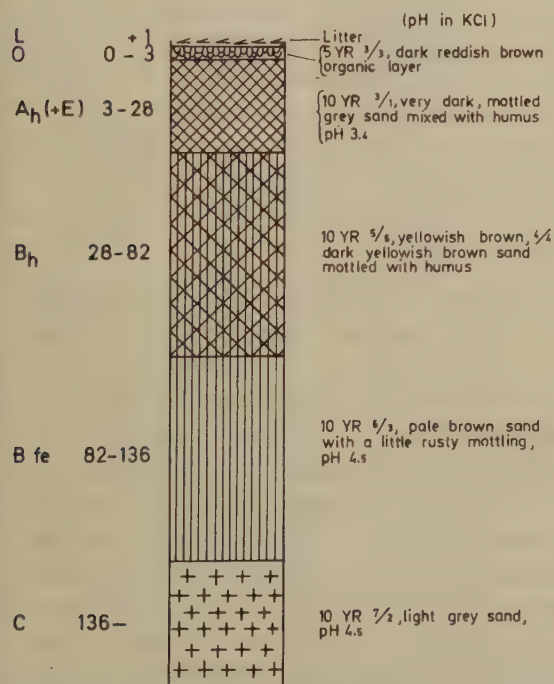


Fig. 24. Soil profile from *Calluna vulgaris* soc. Sandhammaren (1971-4).

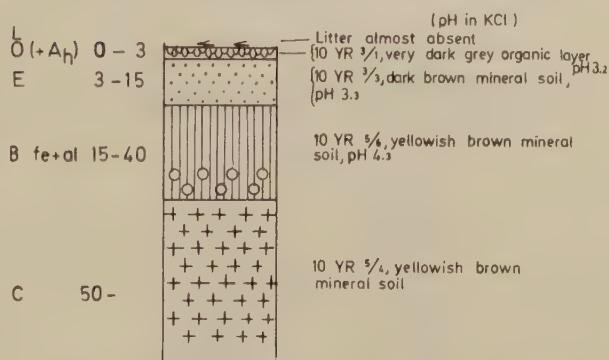


Fig. 25. Soil profile from *Genisto-Callunetum*. Mästocka, S. Halland (1972-5).

podsol in mature stands of *Calluna vulgaris* soc. (Fig. 24) with a dense raw humus and an elongated illuvial B-horizon (Table XXII). The soil profile is different from the condition in a *Genisto-Callunetum* (Fig. 25) also with an eluvial zone on the moraines at Mästocka in the southern part of the province of Halland. The podsolation is still more pronounced in heather areas with scattered pines (Tamm, C.-O. 1947 p. 77). The podsol is often radically changed in the afforested *Deschampsia flexuosa* - *Pinus sylvestris* comm. Two stands, 70 and 30 years old, are investigated (Fig. 26). The stratification is sharper in the first one, also with a second humus horizon. The raw humus layer is thick and rich in roots, in the second stand probably also with remnants of *Calluna vulgaris* and litter ramified with fungal hyphae as in the soil profiles given by Ovington (1951). He has registered a separate distinct horizon of intense reddish brown mottling not seen in the present stands. The afforestation has lowered pH and seems to increase the loss of available nutrients from the soil (see Ovington 1950, 1951). *Vaccinio-Pinetum Empetrum nigrum* subass. on the sandy plain with sea gravels at Haverdal has developed an obvious podsol with both eluvial and illuvial zones (Fig. 27 left), which are sharper in the typical subassociation (see Tamm, O. 1937) on the moraines such as those near Lidhult (Fig. 27 right) in the western part of the province of Småland (Table XXII). The latter soil type is an iron podsol (see Mückenhausen 1962, Kundler 1965).

The oak forest, *Melampyro-Quercetum roboris* *Calamagrostis epigeios* vicariant *Luzula campestris* var., has a podsol with two humus horizons as well as two illuvial B-layers (Fig. 28 left). The inland vicariant is sharply stratified with eluvial and illuvial zones as at Kvarnabacken (Fig. 28 right) in the southern part of the province of Halland (Table

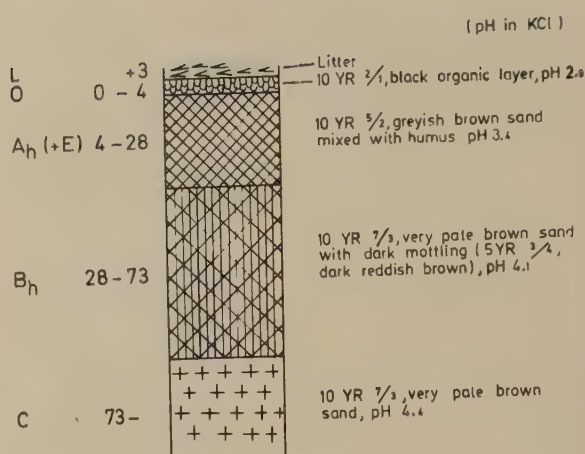
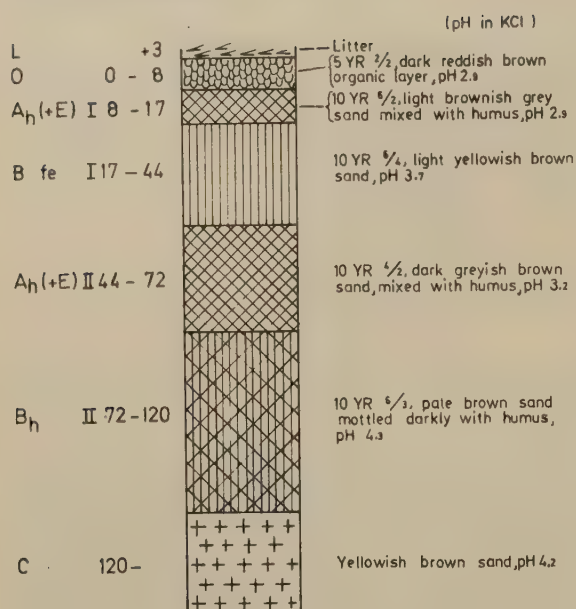


Fig. 26. Soil profiles from *Deschampsia flexuosa* - *Pinus sylvestris* comm. Sandhammaren (1971-4). Left: Stand 70 years old. Right: Stand 30 years old.

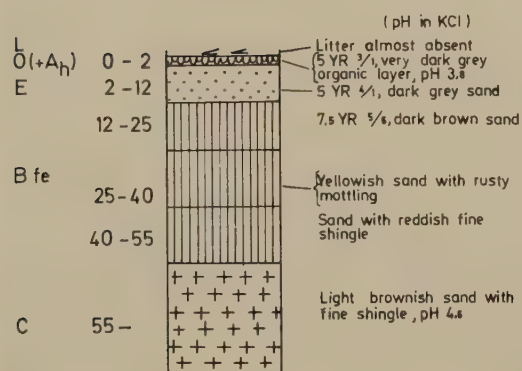
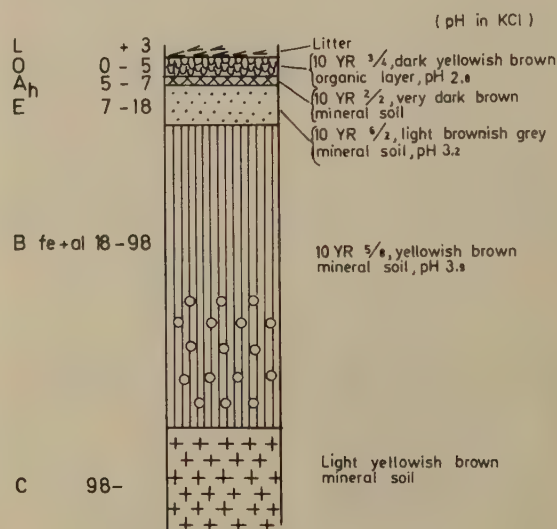


Fig. 27. Soil profiles from *Vaccinio*-*Pinetum sylvestris*. Left: *Empetrum nigrum* subass. Haverdal (1971-11). Right: Typical subass. Lidhult, Småland (1972-5).



XXII), and in the northern part of Scania (Weimarck 1947 c). The oak forest at Sandhammaren has developed a very complicated soil profile partly due to the clone spread (see Feilberg 1968) and sand burial. Also in this subsera there is a decrease in pH from ca. 5 (in KCl ca. 4) in *Cladonio-Corynephorum* to ca. 4 (ca. 3) in the various forests, thus a much smaller decrease compared with the maritime dune subsera, and an increase in organic content.

The glacialfluvial subsera

The glacialfluvial subsera (Fig. 29) comprises the successional evolution on glacialfluvial sand also mix-

ed with aeolian sand and is in some places initiated with a cyclic process between naked sand and pioneer stands of *Senecio vernalis*-*Holcus mollis* comm. and *Teesdalia-Corynephorum*. The latter one is replaced by or in contact with *Antherico-Koelerietum glaucae*, often surrounded by other *Festuco-Sedetalia* communities. *Teesdalia-Corynephorum* is developed chiefly into *Agrostio-Callunetum* and in a later stage *Agrostio-Quercetum roboris*. *Festuca ovina* - *Rumex acetosa* comm. may serve as a separate transitional stage toward *Agrostio-Quercetum roboris*, probably only a subclimax, syn. paraclimax (Tüxen 1951), and with a mixed deciduous forest in climax (see Bjerke 1957).

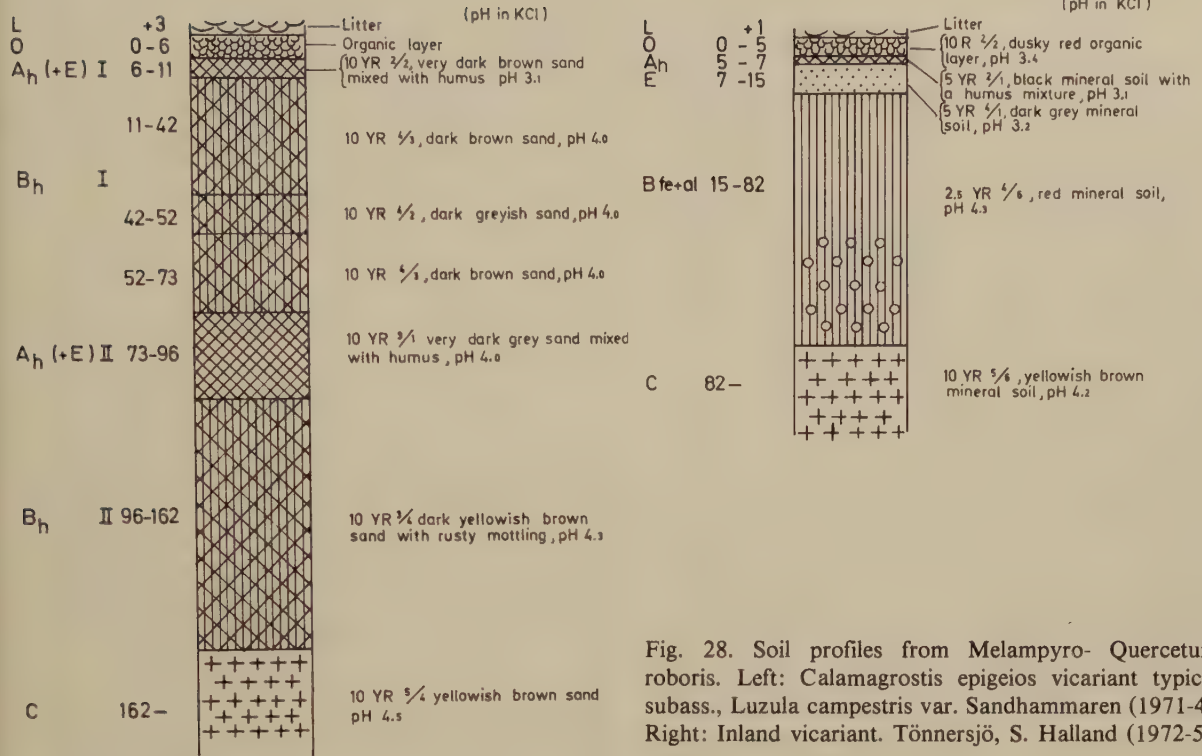


Fig. 28. Soil profiles from Melampyro- Quercetum roboris. Left: Calamagrostis epigeios vicariant typical subass., Luzula campestris var. Sandhammaren (1971-4). Right: Inland vicariant. Tönnersjö, S. Halland (1972-5).

More rarely a *Calluna vulgaris* soc., seen at Revingehed, is a link between Teesdalio-Corynephorum and Melampyro-Quercetum roboris, which occurs mainly on the eskers (see Linnermark 1960) but also on very poor glaci-fluvial sand and is regarded a re-development of an oak forest earlier degraded to a heath (see Tüxen & Diemont 1936). The dwarf shrub heaths on the eskers, corresponding to a Genisto-Callunetum, are today very reduced (Damman 1957, Persson, Å. 1971), invaded by birches (Persson, Å. op.cit. p. 43) or on the hill of Romeleåsen by oaks. Within the series of Agrostio-Quercetum roboris or Melampyro- Quercetum

roboris there are disturbances from various coniferous forests, established outside the natural habitats of pine, Pseudopinetum sylvestris (Passarge 1962 a) a substitute of the oak forest with specific features in the landscape division (Meisel-Jahn 1955). The present author has used Pseudopinetum sylvestris as a name for new afforestations as well as instable stands, often transformed into Agrostio-Quercetum roboris or Deschampsia flexuosa - Pinus sylvestris comm. and affiliated to Vaccinio- Pinetum sylvestris typical subassociation seen at Björka. The two latter forests are also converted into Melampyro- Quercetum roboris.

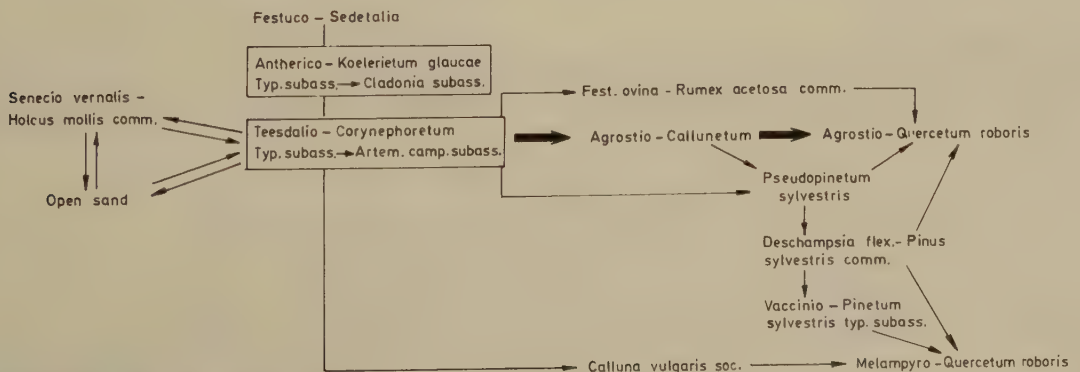


Fig. 29. The xerosere, the glaci-fluvial subsere.

The soil genesis and evolution is here more complicated than on the pure aeolian sands. A progressive trend is found from ranker or podsol-ranker in Teesdalio-Corynephoretum, on the naked sand in certain cases syrosem, towards podsol or podsoloid in mature heath and forest soils. Antherico- Koelerietum glaucae shows a pararendzina (Andersson, O. & Waldheim 1946 Table 6, Waldheim 1947 pp. 67-78, Schlichting 1954 pp. 45-49, Mattiasson 1970, Pålsson, L. 1974). Linnermark (1966) has shown podsolation stages in the pararendzina after coniferous plantations. The heather vegetation influences the soil in different ways. On the moraines there is a pronounced podsol, on glaciuvial sand only podsol-ranker also due to lower precipitation (Damman 1957). Agrostio-Quercetum roboris forms in some places a podsol with a raw humus and an illuvial B-horizon with rusty mottling, in other places a podsoloid lacking a raw humus. Melampyro- Quercetum roboris is more podsolized. Various afforested pine forests have developed on obvious podsol as Galio-Pseudopinetum sylvestris and Deschampsia flexuosa - Pinus sylvestris comm. in Vomb's Fure (Troedsson 1964). There a brown earth during the deciduous era until the 18th century has been successively converted into a soil type similar to a podsol (Troedsson op.cit.) with a deterioration of the soil state as a consequence, also seen at the afforestations at Vitemölla. The leaching of nutrients has accelerated (see Stålfelt 1965 pp. 218-228). The change from brown earth to podsol on sandy soils is the reason for introducing a transitional form, podsoloid (Linnermark 1960). From DDR Kundler (1956, 1961) has discussed the differences between podsol, brown podsoloid soil and brown earth.

THE HYGROSERE

The eutrophic subsere

In this work the hygrosera comprises the vegetation in moist and wet dune depressions with a water-

logged soil, as a rule periodically inundated. The hygrosera has been considered to include one eutrophic (Fig. 30) subsere and one oligotrophic (Fig. 31). In the former besides the hydro factor the air in the soil and supplied nutrients are regarded major factors. The Sparganium minimum comm. is the only true aquatic community depending on a rather permanent water surface. Otherwise the vegetation is converted into a semi-aquatic Caricetum acutae, also a substitute of Irido-Alnetum glutinosae. These two communities are often linked via Alno-Salicetum cinereae. The seral stage Filipendulo-Alnetum glutinosae couples the xerosere with the hygrosera, also evidenced by oligotrophic contact communities, viz., Caricetum canescentis-nigrae, Myrico-Betuletum pubescentis and Athyrio-Alnetum glutinosae. Vegetational stages in a eutrophic subsere can also be seen in the works of Vallin (1925), Fukarek (1961 p. 215), Géhu (1961 p. 261) and Doing (1963 a p. 44).

The oligotrophic subsere

The oligotrophic subsere (Fig. 31) is divided into two series. The first one comprises a zonation found on the west coast from Salicetum arenariae Carex nigra subass. via Molinio-Myricetum gale towards Myrico-Betuletum pubescentis sometimes with Agrostis tenuis - Populus tremula comm. as a transitional link. Many contact communities are present such as Ammophilon borealis, Salici-Empetretum, Cladonio-Callunetum, Vaccinio-Pinion and Caricetum canescentis-nigrae. On Skanör's Ljung Ericion tetralicis has replaced Salicetum arenariae as an initial stage.

In the sense of Good (1935), a very truncated hydrosere is present. He has correlated the seral stages with the increase of water and given a picture of the complexity in this type of habitat. Ranwell (1960 p. 139) has suggested a form of woodland of Quercus and Betula after a stage with Salix and Betula spp. The main soil type is a moist ranker, in

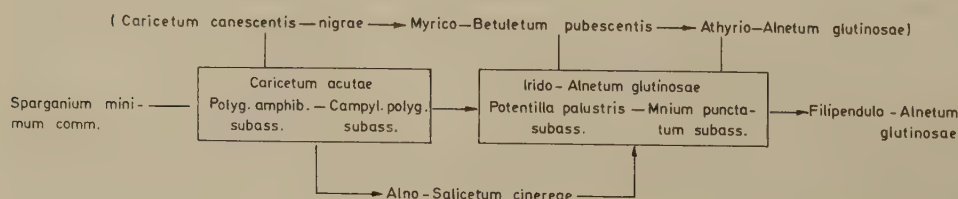


Fig. 30. The hygrosera, the eutrophic subsere.

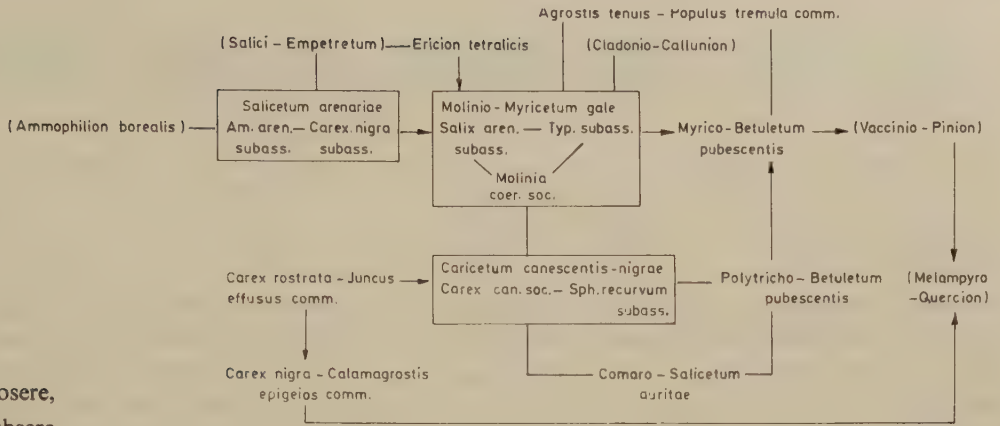


Fig. 31. The hygrosere,
the oligotrophic subsere.

the woodland probably converted into a podsol. In the soil evolution the pH seems to decrease and the organic matter increase (Table XXII).

The subseral development at Sandhammaren is summed up in a second series confined to isolated dune depressions with a high water table (see Walter 1968 Fig. 642). On the wettest habitats *Carex rostrata - Juncus effusus comm.* is established in adjacent wet and moist stands bordering on a mosaic complex including *Caricetum canescentis-nigrae*, *Comaro - Salicetum auritae* and *Polytricho - Betuletum pubescentis* and corresponds to an oligotrophic development with *Sphagnum*-rich communities and *Betuletum pubescentis* described by Fukarek (1961 pp. 235-239) from the peninsula of Darss. In drier habitats *Carex nigra - Calamagrostis epigeios comm.* is a link to *Melampyro - Quercetum roboris*, also in contact with *Polytricho - Betuletum pubescentis*, which seems to be converted into *Myrico - Betuletum pubescentis*. The soil undergoes

very small changes and varies between anmoor fen soil and peat fen soil. The pH varies between 4-5 in the surface soil.

The changes of the climate-phytomorphous soils are easier to study than those of the hydromorphous soils. *Caricetum acutae* could be an aue soil, an allocthonous aue soil (Mückenhausen 1962 p. 122), in some places as in *Caricetum canescentis-nigrae* an anmoor fen soil (Laatsch 1957 p. 264). The alder carrs and the *Salix* tall shrubs have developed on the sand only immature soils as aue soil, anmoor fen soil or in *Irido - Alnetum glutinosae* *Potentilla palustris* subass. a peat fen soil. *Athyrio - Alnetum glutinosae* has a peaty raw humus with a tendency to wet podsol, also observed in *Myrico - Betuletum pubescentis*. Of a quite different origin is a sandy pseudogley in *Filipendulo - Alnetum glutinosae*. There is no seral trend in changes of organic matter and soil reaction.

Vegetational genesis on studied sands

On studying the flora, vegetation and ecology several representative localities have been chosen (Fig. 2) showing important gradients in climate, vegetation and soil.

MARITIME SANDS

Haverdal

The sands extend around the whole bay about 4.5 km in length. Landwards the distance is up to 2 km. The area is divided into north and south parts by a small river, Skintan. Moraine cups are surrounded at the ends of the bay. Arable land and occasional summer cottages border on the sands. The beach is narrow, normally about 30 m and broader only near the outlet of the river, Skintan. The width of the recent dunes is estimated to 50 m and 10 m in height following the shore line. The dunes are succeeded in a transection landwards in the south part by a depression, a wide sandy field mainly with coniferous forests and 1.5-2 km, just near the arable land with old dunes 1.5 km in length, irregular in direction and form. The highest point is 26 m above the sandy plain and 36 m above the sea level. As a whole the dunes describe a curve (see Caldenius et al. 1966 p. 78). About 350 ha of the sands have been preserved as a nature reserve in 1937 (Naturskyddsföreningen . . . 1937, Nordin 1938).

The absence of drift vegetation on the beach is probably a result of seaweed collection. Of interest is the name 'tångallmanning' from earlier time. A poorly developed *Honkenyetum peploidis* occurs just in front of the dunes, somewhere with steep eroded slopes. Near the river outlet a *Cakile maritima* soc. grows on scattered remnants, heaped up near vigorous *Elymo-Ammophiletum*. The continuing process of accretion and erosion has shaped various types of blowouts on the dunes, enlarged by human influence especially in later times. In a work (Betänkande . . . 1936 pp. 63-64) the sands have been divided into five zones, viz., (1) the naked beach, (2) the dunes with marram grass, (3) a zone with shrubby *Pinus mugo*, (4) the forest on a smooth san-

dy plain and (5) the old dunes. From the sands south of Falkenberg Améen (1962) has separated three main zones, viz., (1) the beach, (2) the *Ammophila* dunes and (3) the sandy field with gray dunes split into a) the forest, b) the inundated depression and c) the heath. Compared with the dune systems on the island of Læsø and at Skagen, the spit of Jutland (see Böcher 1941 b, 1952), the two outer zones at Haverdal, the beach and the dunes, are small and with fragmentary plant communities. Stable *Cakiletum maritimae* and *Elymo-Agropyretum junceiforme* seem to be absent. At Haverdal, also at Tönnersa, *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass. occurs on the leesides of the dunes as well as on places exposed to erosion. In some places it is located more seawards than the typical subassociation which is only thriving with enough sand burial. In the accretion zone of the blowouts there may be an *Ammophila arenaria* soc. On less exposed places a closed *Agropyro-Rosetum rugosae* is in contact with *Elymo-Ammophiletum*, rarely with *Ammophila x baltica*. On steep slopes on the northern part of the back dunes there is an *Agrostis tenuis* - *Populus tremula* comm., streamlined by the wind, in certain stands with *Rhamnus frangula* as a subdominant and other nano-phanerophytes such as *Betula* spp., *Salix* spp. and *Crataegus* sp. of minor importance. Various graminids such as *Agrostis tenuis*, *Carex arenaria*, *Anthoxanthum odoratum*, *Poa pratensis* and *Deschampsia flexuosa*, are constituents of a rather open field layer.

On sheltered places small patches of *Violo-Corynephorretum*, both typical subassociation here marked with *Artemisia campestris*, *Galium verum* and *Thymus serpyllum* and *Cladonia* subass., are in a mosaic with *Salici-Empetretum Festuca arenaria* subass. forming intensively green carpets, also seen at Östra Stranden south of Halmstad. Although rare finds of *Cladonia dstricta* are noticed no *Cladonio-Corynephorretum* is observed as on the island of Læsø (Böcher op.cit. Table 8). *Cladonia alpicornis* is striking. On sands strongly affected by man, as at

Ringenäs on the bay Tylösandsbukten, a Teesdalio-Corynephorum is present with *Rumex tenuifolius*, *Thymus serpyllum*, *Agrostis tenuis*, *Aira praecox* and *Festuca ovina* joining vital individuals of *Corynephorus canescens* and *Carex arenaria*. A specific floristic structure of *Salici-Empetretum* is recorded near the village of Haverdal on low back dunes, where a mixture of *Juniperus communis*, *Rosa rugosa* and *Lotus corniculatus* appears. On low dunes near the village of Villshärad small shrubby stands with *Pinus mugo* are present.

Of special character is the vegetation along the small river, Skintan. The water is contaminated and rich in nutritive substances. Near the outlet a mixed stand very rich in plants such as *Potentilla reptans*, *Polygonum amphibium*, *Phalaris arundinacea* and *Phragmites communis* occurs. Near the water tall shrubs of *Salix* spp. are found. A *Filipendulo-Alnetum glutinosae* is situated on a ground rich in fine sediments forming a pseudogley, as at Tönnersa. The trees are low-growing and the canopy is shaped by the wind. The herbaceous layer is very well developed. Upstream there is another forest belonging to *Geranio-Fraxinietea* and characterized by the presence of *Impatiens grandiflora*.

Between the outer dunes and the forest zone there is a depression, the lowest part in the whole dune system, which is inundated in winter. Physiognomically this area is a vegetation complex. The driest stands are occupied by *Salici-Empetretum* with scattered *Erica tetralix* and *Lotus corniculatus* with red and yellow flowers, accompanied by *Carex nigra*, *C. panicea* and *Plantago maritima* on small elevations or on the gentle slope with virgin pines inside the depression. Here the main part of the vegetation belongs to *Molinio-Myricetum gale* *Salix arenaria* subass. forming a series of variants after a hydro gradient. The homogeneity is decreased. Just behind the outer dunes on rather dry sites *Vaccinium uliginosum* forms closed stands. The presence of *Potentilla anserina* and *Filipendula ulmaria* is a result of the instable conditions. *Erica tetralix* dominates where the water has difficulties in infiltrating. The liverwort *Gymnocolea inflata* grows in the interspaces and indicates certain agreements with *Ericetum tetralicis*. However, the floristical structure is very different from a wet heath vegetation as at Skanör's Ljung (see Malmer et al. 1965 pp. 129-130) or at the small village of Steninge north of the investigated area (see Böcher 1943 a Table 22), where

the situation is more similar, although lacking in *Myrica gale*. Related vegetation from Jutland (Raunkiaer 1914, Heyken 1965 Table 38) and from the Netherlands (van Dieren 1934 Table 51) is found. Scattered small *Sphagnum recurvum* hummocks with *Oxycoccus palustris* and *Molinia coerulea* occur, probably a more western feature. In the vicinity of the wettest part in the gradient *Myrica gale* grows together with *Potentilla palustris*, sometimes *P. anserina*, and *Agrostis canina*. The two latter ones indicate a relationship with *Agropyro-Rumicion* (Westhoff & Den Held 1969 p. 110). In an adjacent stand *Phragmites communis*, *Carex nigra* and *Naumburgia thyrsiflora* are found. On the most inundated place there are also *Iris pseudacorus*, *Lythrum salicaria* and *Lysimachia vulgaris*. A *Nardetalia* community with *Nardus stricta*, *Deschampsia flexuosa*, *Potentilla erecta*, *Luzula multiflora*, *Viola canina* and *Veronica chamaedrys* occurs on the north side of the small river in a fringe behind the outer dunes, near a small fen of *Caricetum canescentis-nigrae* *Calamagrostis canescens* variant joining *Juncus filiformis*, also seen at Tönnersa.

A fragment of *Molinio-Myricetum gale* typical subassociation with *Myrica gale*, *Vaccinium uliginosum*, *Juniperus communis*, *Potentilla erecta* and *Molinia coerulea* forms a pioneer dense shrub vegetation between the depression marked with *Salix arenaria* subass.; when streamlined it is transformed into an instable *Agrostis tenuis* - *Populus tremula* comm. with a low canopy of *Populus tremula* and *Rhamnus frangula*. *Vaccinium vitis-idaea*, *Deschampsia flexuosa* and *Melampyrum pratense* appear in the undergrowth. *Myrico-Betuletum pubescentis* in higher stands is in contact landwards. A related zonation is given by Nilsson, N.-G. (1966) from the coast at Steninge. The main part of the sandy plain is covered by *Vaccinio-Pinetum sylvestris* *Empetrum nigrum* subass. on a gentle slope near the depression colonized by *Salici-Empetretum* with juvenile individuals of both *Pinus sylvestris* and *P. mugo*. The pine forest consists, in the stage immediately after *Salici-Empetretum*, of very thin, rather scattered pines with a mosaic of *Empetrum nigrum* and *Cladonia* spp. on the ground (see Wojterski 1964 b). The soil condition is very complicated with a fine shingle stratification leading to the poor podsolated stands. Probably the aeolian sand has been removed to a large extent and accumulated in



Fig. 32. The maritime sands at Haverdal. E = Lynga dune, F = a lake, today only a marsh. Map drawn by Kanter in 1750.

the old dunes. Kanter (1750) has marked a large area with 'klappersten' (=fine shingle) and aeolian sand partly surrounded by smooth heather vegetation. Landwards on well-sorted aeolian sand a moss-rich pine forest is present. In a *Quercus petraea* sub-ass. the pines are mixed with *Picea abies*, *Betula pubescens* and *Quercus petraea*. *Vaccinium* spp. have replaced *Calluna vulgaris* and *Empetrum nigrum*.

On and behind the old dunes, which caused the people considerable trouble (see Söderlingh 1698, Kanter loc.cit., Olsson, A. 1940-45), *Quercus petraea* is predominant. An oak forest seems to have covered parts of the sands in earlier time (see Richardsson 1752-53 p. 184). On the dunes the oaks are shrubby and in some places mixed with *Tilia cordata* and *Juniperus communis* and with various acidophytes, such as *Luzula pilosa*, *Trientalis europaea* and *Deschampsia flexuosa* in the field layer. The absence of *Calamagrostis epigeios* indicates closer relationships with inland poor oak forests than with the coastal vicariant at Sandhammaren. On the highest dunes isolated clones of *Amphiphila arenaria* are present. The pine forest, also with certain young plantations, extends seawards.

Inside the dunes the oak forest, with a podsoloid and influenced by man, contains both heath and meadow plants, such as *Convallaria majalis*, *Oxalis acetosella* and *Anemone nemorosa*. Both Söderlingh (op.cit.) and Kanter (loc.cit.) have described a lake between the dunes and the arable land. The lake today is reduced to a contaminated marsh.

Tönnersa

A wide area of aeolian sand is situated around the outlet of the river Lagan and landwards estimated to 1150 ha or more by Noreen (1891). The distance along the shore between the outlets of the two rivers, Lagan and the northern Genevadsån, is about 4 km. The sand is on the broadest part 4-5 km, but only 1.5 km wide in the southern part of the bay Laholmsbukten. The beach is 30-40 m in width. The recent dunes following the shore line are 100 m broad and 5-10 m in height. The depression immediately inside the dunes, very pronounced in the southern part, marks the place of an embanked shore lake (Öster 1952 p. 201). A second dune ridge, 10-13 m in height, is situated about 300 m from the seashore. The main part of the sands closer to the arable land is composed of a plain with a pine forest. Old dunes are built up in the E-SE part, 3-4 km from the seashore, 10-15 m above the plain and about 25 m above the sea level (see Mohrén & Larsson, W. 1968 p. 85). The topography is irregular in a NNE-WNE direction. In some places in the arable land, today intensively cultivated, the village landscape is formed with smooth sand dunes covered with grass and with scattered oaks (see Sjöbeck 1945). South of the river mouth of Lagan the outer recent dunes are successively decreased in size in the direction towards the village of Skummeslöv. North of the river mouth of Genevadsån the dunes are in contact with moraine cups. About 400 m from the seashore a motorway separates the sands.

Near the outlet of the river Lagan the width of the beach is strongly variable as a consequence of changes in supplied water volumes from the river, leading to an abrasion process often in combination with the erosion effect from the storms. The beach is naked without wrack deposits, very different from the situation at the northern part on the beach bar near the outlet of the river Genevadsån. A dune plateau borders on the beach bar and extends southwards abruptly edging smaller dunes, slowly accumulating or nearly constant in height with a



Fig. 33. Eroded dunes. Tönnersa 1973. Photo B. Wallén.

monotonous vegetation of *Elymo- Ammophiletum*, near the river mouth of Lagan. Near the beach *Ammophila arenaria* is robust and vital. On stable sand *Ammophila x baltica* occurs in separate clones, more rarely also *Calamagrostis epigeios*. A *Salicetum arenariae Ammophila arenaria* subass. in some places borders inwards on the flat, wide dune depression. On certain lee slopes degenerated stands are rich in bryophytes and lichens, such as *Ceratodon purpureus*, *Pohlia nutans*, *Brachythecium albicans*, *Parmelia physodes*, *Cetraria glauca*, *Usnea hirta*, *Evernia prunastri* and *Cladonia* spp. *Polypodium vulgare* is absent and no agreements with *Salici-Empetretum* are found.

The dune plateau is broken with many blowouts and steep eroded slopes, especially towards the beach (see Bergström 1968). The wind breaches have formed small barchans with sand volumes transported in over the depression. The normal succession is interrupted. The sand burial favours the *Ammophila arenaria* soc. in monospecific stands. On steep slopes on back dunes with loose sand *Festuca arenaria* is mixed. On firm sand the *Hieracium umbellatum* spp. subass. is present, often on the eroded dunes near the beach. On places with reduced or without sand supply relicts of *Violo-Corynephorretum Cladonia* subass. occur as a rule on a mat of rapidly colonizing *Polytrichum piliferum* (see Warming 1909 p. 237). Green carpets of *Empetrum nigrum* soc. are in a mosaic and expand over the lichen-rich stands, also as a result of too great supply of sand superseded by *Ammophila arenaria*.

Juvenile pines are scattered on the dunes, often near fragments of *Salici-Empetretum Lophocolea*

heterophylla subass. Round certain pines on the bare ground a form of *Cladonia alpicornis* with large phylloclads is seen. *Salix arenaria* thrives in continuous sand burial, studied near a small depression, a slack, in connection with the flat, wide depression through a narrow furrow. A wind breach has pushed sand in over the slack dominated by *Salicetum arenariae Carex nigra* subass. On the new sand *Salix arenaria* grows vigorously, prostrate up to half a metre, an expanding clone in the *Salix arenaria* cycle (see Paul 1944 pp. 328-337, Ranwell 1960 p. 130), here illustrating the accretion phase.

In the wettest corner of the slack, towards the sea, a *Molinio- Myricetum gale Salix arenaria* subass. has been mixed with elements from *Caricetum acutae*. Today this stand is buried by sand. Certain plants from *Ericion tetralicis*, such as *Erica tetralix* and *Lycopodium inundatum*, have been seen in instable habitats often edging the slack. A related milieu is reported from Hökafältet south of the river Lagan (Nilsson, A. 1905 p. 330). *Salicetum arenariae Carex nigra* subass. contains scattered *Carex acuta*, the furrow *Iris pseudacorus*, and certain dune walls climbing *Phragmites communis*. A good indicator of the fluctuating water condition is *Achillea ptarmica* edging the slack, furrow and the flat wide depression, in the central part separated by a ditch, rather parallel to the shore line, with *Carex rostrata*, *Alisma plantago-aquatica* and *Ranunculus flammula*. Along the ditch and edging the dunes seawards there is an *Alno- Salicetum cinereae* (see Passarge 1961, Doing 1962, Passarge & Hofmann 1968), ranked with *Carici- Salicetea cinereae*, with wind-shaped and streamlined canopies. The most important tall shrub



Fig. 34. Vegetation mosaic in a wide depression inland from the seaward dunes. Alno- *Salicetum cinereae*, *Caricetum acutae*, *Caricetum canescentis -nigrae* and in the background *Myrico-Betuletum pubescentis*. Tönnersa 1971. Photo H. Olsson.

is *Salix cinerea*, often mixed or surrounded with *Phragmites communis*. *Alnus glutinosa*, *Populus tremula*, *Betula* spp. and *Salix aurita* are in subordination. *Caricetum acutae* is in the wetter parts differentiated into a monotonous *Polygonum amphibium* subass., on somewhat drier stands into a *Campylium polygamum* subass. Landwards a *Caricetum canescentis -nigrae* *Calamagrostis canescens* variant is present succeeded by a transitional zone with dead trees and a specific flower spectrum of white, yellow, blue and red colours from *Peucedanum palustre*, *Lysimachia vulgaris*, *Scutellaria galericulata* and *Lythrum salicaria* in a direction towards *Myrico-Betuletum pubescentis* on higher ground, sometimes preceded by an aspen tall shrub.

The forest undergrowth consists of a nano-phanerophyte layer of *Myrica gale*, *Vaccinium uliginosum* and *Populus tremula* and a well-developed moss carpet. On the steep slope of the second dune ridge *Carex arenaria*, scattered *Ammophila arenaria* and *Hieracium umbellatum* ssp. are seen, on the top a light *Cladonio-Pinetum sylvestris* *Corynephorus canescens* subass. Adjacent to the last-mentioned a shrubby *Pinus mugo* stand occurs. Further inwards *Vaccinio-Pinetum sylvestris* *Empetrum nigrum* subass. appears in three phases, the first moss-rich one dominated by *Pleurozium schreberi* on a smooth ground, the second in rather dark habitats with *Empetrum nigrum* as the only chamaephyte and the third marked with *Vaccinium vitis-idaea*. In the

terrain depressions *Myrico-Betuletum pubescentis* is uniformly triple-layered with *Betula pubescens*, *Myrica gale* and *Hylocomium splendens*, in certain cases also *Ptilium crista-castrensis*. A birch fen with *Carex nigra* and *C. canescens*, similar to a *Polytricho-Betuletum pubescentis*, is less common.

Just behind the outer dunes, about halfway to the river Genevadsån an alder carr, *Irido-Alnetum glutinosae* is periodically inundated and supplied with allochthonous humus. An adjacent *Alno-Salicetum cinereae* is very closed and the undergrowth nearly absent, only with a naked dark humus ground, although *Caricetum acutae* grows outside. On a back dune an *Agrostis tenuis* - *Populus tremula* comm. with the nano-phanerophytes *Populus tremula*, *Sorbus aucuparia* and *Rhamnus frangula*, with a field layer of *Maianthemum bifolium* and *Agrostis tenuis* corresponds to an analyzed stand at Ängelholm. An *Athyrio-Alnetum glutinosae*, more common on the moraines (see Malmström 1937), as well as a *Sphagno-Alnetum glutinosae* (see Malmström op.cit., Malmer 1968 c), recognized by the presence of *Athyrium filix-femina* and an increased frequency of *Betula pubescens* compared with *Irido-Alnetum glutinosae*, occupies a soil with a rather peaty surface layer and extends to the north near the river Genevadsån where it is replaced by *Filipendulo-Alnetum glutinosae*.

The northernmost dune area is characterized by a beach bar, the flattest part naked or sparsely colonized by *Honkenya peploides* and *Elymus*



Fig. 35. The maritime sands at Tönnersa, with shrubby fences both on seaward dunes and old inner dunes. Map drawn by Kanter in 1750.

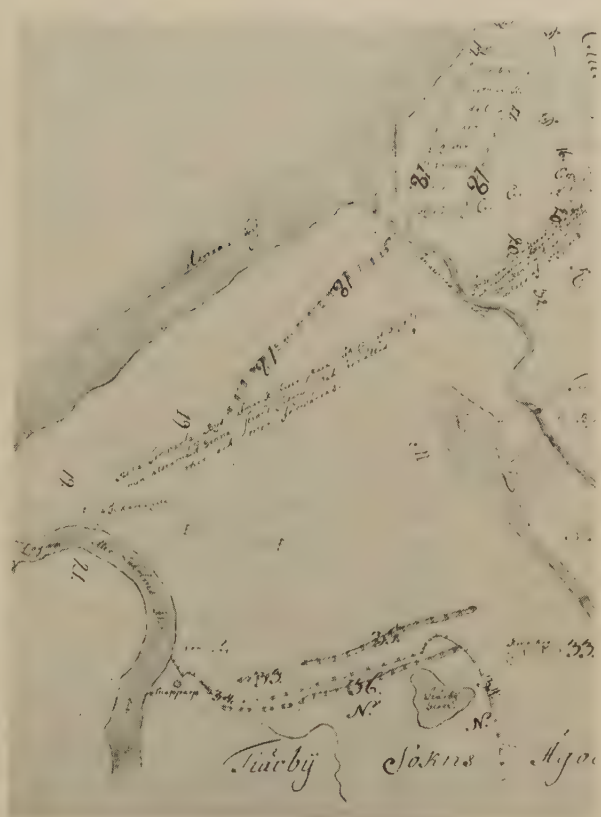


Fig. 36. The maritime sands at Tönnersa. Map drawn by Söderlingh in 1691 (1709).

arenarius (see Ardö 1957 Fig. 32). The shell deposit is small and much less compared with the situation at Ängelholm. Cast-up seaweed has developed a substratum for *Cakile* *maritima* or *Atriplicetum* *littoralis* and there is also a *Cakile* *maritima* soc. on isolated drift material. Just outside the low primary dunes with *Ammophila* *arenaria* and scattered *Agropyron* *juncum* ssp. *boreoatlanticum*, a fringe of *Honkenya* *peplodes*, 5-10 m in width, extends separated from the wracks situated nearer the sea water line. *Elymo*-*Ammophiletum* *Hieracium* *umbellatum* ssp. subass. grows on a steep slope of a second dune row up to the dune plateau. Also on other places in the broken dune landscape, on rather sheltered firm sand *Hieracium* *umbellatum* ssp. and *Parmelia* *physodes* are very striking. An isolated stand contains *Festuca* *ovina* and *Scleranthus* *perennis*. Clones of *Ammophila* *x* *baltica* occur only here and in the southernmost part of the dune area. *Violo*-*Corynephorretum* and *Salici*-*Empetretum* are in a mosaic, also with wide blowouts. At the end of wind furrows vigorously growing *Ammophila* *arenaria*

soc. is striking. *Violo*-*Corynephorretum* typical sub-association contains *Festuca* *arenaria*, *Artemisia* *campestris* and *Viola* *canina* var. *dunensis*, more vital in a narrow zone bordering the *Empetrum* *nigrum* carpets, degenerated into *Cladonia* *subass.*, more common in the south part of the dune area. *Salici*-*Empetretum* *Festuca* *arenaria* subass. or *Empetrum* *nigrum* soc. colonizes *Violo*-*Corynephorretum* where the leaching of the soil advances. The *Empetrum* patches grow larger where the soil is covered with a lichen carpet and merge into an *Empetrum*-*Cladonia* heath (Böcher 1943 a p. 46). The *Empetrum* *nigrum* stands are colonized by *Calluna* *vulgaris* in later stages, giving the *Lophocolea* *heterophylla* subass. in the western region with *Lotus* *corniculatus* (see Raunkiaer 1914 Table 8, Böcher 1941 b Table 2), where the sand accretion has ceased, rather close to the river Genevadsån. On the wet sand along the river there are certain plants that are found on sandy shores of the lake Vänern (see Norén 1906). Reeds of *Typha* *latifolia*, *Carex* *acuta* and *Juncus* *maritimus* are

replaced by an Alno- *Salicetum cinereae* inside, with a meadow margin vegetation of *Filipendula ulmaria*, *Succisa pratensis*, *Rumex acetosa*, *Plantago lanceolata*, *Holcus lanatus*, *Fragaria vesca* and *Vicia cracca*. At the place where the river turns to the north a wind breach is very pronounced and large quantities of sand have moved out into the river, which probably will soon resume its old direction straight to the sea, which can be seen on old maps (Söderlingh 1691, Kanter 1750, Brandberg 1819). Upstream in the vicinity there is a *Filipendulo-Alnetum glutinosae*, in certain stands with *Humulus lupulus* climbing on the tree trunks, on drier ground with *Paris quadrifolia* and *Impatiens parviflora*, on somewhat better with *Thalictrum flavum* and *Valeriana sambucifolia*. The northernmost locality of *Dianthus superbus* is found in the surroundings (Hallenborg 1956).

In the area of old dunes, marked as a shrubby fence by Kanter (op.cit.), *Cladonio- Pinetum sylvestris*, both typical subassociation with *Cladonia rangiferina* and *Corynephorus canescens* sub-association, occurs fragmentarily on the dune tops. *Vaccinio- Pinetum sylvestris Empetrum nigrum* sub- ass. is found on moister habitats rich in *Vaccinium vitis-idaea*, in some places with fewer nano-chamaephytes and with an increased moss cover. Of the dwarf shrubs *Calluna vulgaris* is uncommon. The human influence can be seen in a pine stand with small planted *Picea abies*, and with drainings and clearings. The forest also with *Myrico- Betuletum pubescentis* on the sands has changed the substrate from dry, when the area was covered with heather (see Söderlingh op.cit.), to hygric favouring *Ledum palustre* at its westernmost locality (Nordin 1941). *Linnaea borealis* immigrated 30-40 years after the main pine plantation (Neumann 1884 p. 12).

Ängelholm

In the inner part of the bay Skälderviken, a wide dune area is situated between the outlet of the small river Rönneån, near the town Ängelholm, and that of Vegeån, near the village of Vegeholm. The sands cover an area of about 800 ha (Lindbohm 1891). The recent outer dunes are low, especially in the direction towards the river Vegeån. Near the river mouth of Rönneån the dunes are about 5 m high, situated on a beach bar as a result of the altered course of the river similar to the situation in the

northern part of Tönnersa. The inner dune landscape is somewhat wavy dominated by coniferous plantations. Old dunes according to Nilsson, A. (1905), are found at a distance of 0.7 and 1.3 km from the seashore, and, according to Lindström (1884), have probably originated from beach ridges. It is more conceivable that these dunes are a result of human action (Linné 1749, Lindbohm op.cit.). Landwards the sands border on the arable land, the town of Ängelholm and small villages. Several roads and a railway cross the area. Fellings and drainings are going on. In 1953 44 ha of the outer dunes were made into a reservation.

The beach is mostly naked up to a line with drift materials heaped up by the winter storms and occupied by *Honkenyetum peploidis*, in a green fringe 5-10 m in width, in some places by an *Agropyron x acutum* variant (see Gravesen & Vestergaard 1969 p. 72), only recognized here. On the naked beach a fragment of *Atriplicetum littoralis* may be seen. The shell deposits seem to favour an *Honkenyetum peploidis* in a contact with *Elymo-Ammophiletum* mixed with various nitrophytes, such as *Rumex crispus*, *Solanum dulcamara* var. *marinum*, *Sonchus arvensis* and *Agropyron repens*. Present plants have agreements both with *Agropyreteia pungentis* (Géhu & Géhu 1969) and with *Agropyro- Rumicion crispi* (Nordhagen 1940). Böcher (1952 b) has studied the vegetational development in relation to marine accretion and shown the importance of *Honkenyo-Crambion maritimae* communities. Only *Honkenyetum peploidis* occurs at Ängelholm, where probably a very reduced *Agropyron pungentis* (Géhu & Géhu op.cit.) syn. *Angelicon littoralis* (see Westhoff & Den Held 1969), is found with nitrophilic perennials. In the mesohalinic zone on the very flat outermost dunes, physiognomically similar to *Elymo-Ammophiletum* although *Elymus arenarius* is predominant (see Ringdahl 1921), there are in certain stands *Urtica dioica*, *Chamaenerion angustifolium*, *Iris pseudacorus* and the moss *Brachythecium rutabulum*. In habitats with a greater drift mixture in the sand *Aegopodium podagraria*, *Galium aparine*, *Angelica archangelica* ssp. *littoralis* and *Senecio vulgaris* occur. *Potentilla anserina* is rather uncommon and a *Potentillo- Elymetum* (see Hallberg 1971) is not present. An indication of a more stable condition is the establishment of *Agrostis tenuis*, and *Festuca arenaria* and to a lesser extent *Poa pratensis* at Falsterbo.

On the higher dunes towards Ängelholm the floristic structure is different in the *Pleurozium schreberi* - *Agrostis tenuis* comm. physiognomically determined by *Deschampsia flexuosa* and *Carex arenaria*, also with *Corynephorus canescens*, *Aira praecox* and *Agrostis tenuis* and on back dunes *Dryopteris spinulosa* juv. and *Polypodium vulgare* showing a very acid soil reaction. Isolated clones of *Ammophila x baltica* as well as of *Calamagrostis epigeios* are seen adjacent to *Ammophila arenaria* stands in a mosaic with the previous community. 'Islands' of *Rosa rugosa* complete the picture. Towards the Vegeholm plain dense stands with *Carex arenaria*, scattered with *Stellaria graminea* and *Asparagus officinalis*, and a well-developed moss layer may border on a *Nardetalia* community with *Nardus stricta* and *Potentilla erecta*, in a low narrow fringe. They may also be adjacent to *Salici-Empetretum Polypodium vulgare* subass., often as patches on back dunes but also exposed on the front side. *Polypodium vulgare* subass. is here characterized by the combination of *Empetrum nigrum* and *Polypodium vulgare* together with *Parmelia physodes*, *Peltigera canina*, *Cladonia* spp. and various bryophytes and is obviously differentiated from the *Lophocolea heterophylla* subass. on dry stands outside the pines dominated by *Calluna vulgaris* and with occasional *Potentilla erecta*.

On places sheltered by the trees with an increased moistness *Salix arenaria*, *Lotus corniculatus*, *Sieglingia decumbens* and *Erica tetralix* are included as constituents. To the first type of stands a *Cladonio-Corynephoretum* could be linked with a dark-coloured ground of *Cetraria crispa*, *C. islandica* and *Cornicularia aculeata* mixed with scattered *Polytrichum piliferum* and *Cladonia pleurota*, at Ängelholm with weak agreements also with *Violo-Corynephoretum* and *Teesdalia-Corynephoretum*.

Seedlings of *Betula verrucosa*, also seen at Sandhammaren and at Skanör's Ljung, colonize the dwarf shrub heath and in later stages develop into a low-growing *Myrico-Betuletum pubescentis* with both *Betula verrucosa* and *B. pubescens*. Of special interest is a plant community where the hygric climate has favoured a constellation of *Erica tetralix* and *Vaccinium uliginosum*, furthermore with *Nardus stricta* and *Juncus balticus*. It is similar to a stand on Östra Stranden just south of Halmstad (Ardö 1957 p. 50). A fragmentary *Erica tetralix* community along the Swedish west coast from Steninge (see

Böcher 1943 p. 85, Nilsson, N.-G. 1966) to Ängelholm corresponds to an *Empetro-Ericetum* (Westhoff 1947, Westhoff & Den Held 1969) with *Juncus balticus*, *Salix arenaria* and *Empetrum nigrum* as differential taxa and differs from another *Ericion tetralicis* community on Skanör's Ljung (see Tyler et al. 1973 Table 1). *Empetro-Ericetum* is divided into a Baltic *Juncus balticus* race (Hueck 1932, Libbert 1940) with a northern outpost along the Swedish west coast and a western *Juncus anceps* race extending from the Netherlands to Jutland (Westhoff 1947, Raunkiaer 1914 Table 7). *Juncus balticus* is also found in moist sandy deflations, as seen at Tönnersa, growing together with *Juncus filiformis* and different fungi.

In a wind furrow near a coniferous stand including *Pinus sylvestris*, *P. mugo*, and *Picea glauca* (see Sylvan 1892 pp. 30-33) the moist sand is colonized by *Salix arenaria* and *Agrostis stolonifera* with *Ceratodon purpureus* and *Pohlia nutans* as striking bryophytes. *Salix arenaria* immigrates from the moist furrow, to surrounding *Salici-Empetretum*, landwards replaced by *Vaccinio-Pinetum Empetrum nigrum* subass., separated into various phases, in light stands with *Calluna vulgaris*, on places with preserved moistness *Vaccinium vitis-idaea* and *V. uliginosum* rarely bordering on a *Pyrolo-Pinetum sylvestris*. A mixed forest of *Pinus sylvestris*, *Picea abies* and to a lesser extent *Fagus sylvatica* rather well regenerated can be seen adjacent to a dense spruce forest. In the two latter types there is *Vaccinium myrtillus*.

Behind the outer dunes on the central parts there is a pond largely covered with reeds of *Phragmites communis*. This is surrounded by *Alno-Salicetum cinereae* also with *Magnocaricion* plants (see Passarge 1956 b, Passarge 1961, Passarge & Hofmann 1968) normally replaced by *Irido-Alnetum glutinosae*, in certain stands well developed with *Carex elongata* tussocks, on drier soil in contact with *Rubus idaeus* and *Urtica dioica* and in wet oligotrophic habitats with a *Potentilla palustris* subass., rarely with *Carex lasiocarpa*. In extremely wet milieu the alder carr contains *Hottonia palustris* (see Gustavsson 1968), which is similar to the situation on the island of Halland's Väderö (see Vallin 1925). Between the pond and the dunes there is an elongated groove, which is filled with water most of the year. Many observed sedges, *Carex acuta*, *C. acutiformis*, *C. elata* and *C. pseudocyperus* (see

Gustavsson op.cit.), indicate the eutrophic milieu also with the nymphaeid *Sparganium minimum* comm.

Compared with the poor oligotrophic dune depressions at Sandhammaren the corresponding ones on the west coast from Haverdal to Ängelholm are eutrophic and rich in plants as a consequence of the inundation. On a slope near the groove an *Agrostis tenuis* - *Populus tremula* comm. occurs. Besides the predominant *Populus tremula* also the nano-phanerophytes *Sorbus aucuparia*, *Rhamnus frangula*, *Rosa* spp. and *Crataegus* sp. are found. Landwards *Myrica*-*Betuletum pubescentis* with *Molinia coerulea* and scattered *Dryopteris spinulosa*, mixed with *Mnium hornum* covered lumps occur. *Cornus suecica* is rare. On the dune ridges *Quercus robur*, sparsely found, shows a good regeneration. In the margin of the sands a *Melampyro*-*Quercetum roboris* inland vicariant occurs.

Falsterbo

The shores along the Sound are characterized by very small dunes and reduced sand accretion. Instead the supply of drift materials favour various halo-nitrophytes of *Agropyreteea pungentis*. North of the town of Hälsingborg a relict oak forest (Sjöbeck 1923) grows on a fixed dune. The forest, earlier with a wider extension, began to disappear more than 400 years ago. Now there are shrubby stands of *Quercus robur*, *Corylus avellana*, *Sambucus nigra*, *Crataegus* spp. and *Lonicera periclymenum* with a well-developed herbaceous field layer rather similar to oak woods on Jutland (see Gram et al. 1944) surrounded by heaths composed of *Empetrum nigrum* and *Corynephorus canescens*.

The peninsula of Falsterbo is built up by a series of beach ridges connected to each other. On the western side the isthmus is 7.5 km from the northern spit to the southern one, Ugglénabben, further elongated by Falsterbo reef, and 7.5 km (Richter 1936 Fig. 22) to the small island Måkläppen. The narrow central part of the peninsula separates the bay Höllviken on the north side and the smooth bays Ammebukten and Kämpingebukten on the south side. Outside the town of Falsterbo-Skanör lagoon lakes occur parallel to beach ridges. The pattern is partly destroyed by man through fillings for golf links. New reefs and isolated lagoons are still developed as seen on the island of Måkläppen (Davidsson 1963 Fig. 39). Moreover the configura-

tion of the coast line is changed. According to Nelson (1923) the south spit Ugglénabben, has moved 300 m in a SW direction during half a century. The main part of the peninsula, about 2 m above the sea level and 10 km in width, is a deflation area and high dunes have never been found except at Falsterbo Church, where a dune up to 10 m has been recorded (Söderberg 1903 p. 53). Kock (1765) has pointed out that the town of Skanör is situated somewhat higher than the surroundings and protected from severe floods by large parts of the isthmus.

On the south side of the spit Ugglénabben a small fringe of *Honkenyetum peplidis* occurs, moreover on the west side *Atriplicetum littoralis* and a *Cakile maritima* soc. The dunes are low, 2-3 m, overgrown with *Elymo*-*Ammophiletum*, here composed of *Ammophila arenaria*, *A. x baltica*, *Elymus arenarius* and *Agropyron junceum* spp. boreoatlanticum, of which the two latter ones may belong to a fragment of the Atlantic *Elymo*-*Agropyretum junceiforme*. *Honkenyo*-*Agropyretum acuti* borders on the outermost spit, where the drift supply has favoured *Elymus arenarius*. A guanotrophic vegetation on the island of Måkläppen (Gertz 1933, 1948) is related, as well as an offshore barrier community south of Copenhagen (Gravesen & Vestergaard 1969). A *Lepidietum latifolii* (see Dahlbeck 1945) completes the register of *Agropyreteea pungentis* communities. An expanding weakly nitrophilic *Agropyro*-*Rosetum rugosae* also with *Asparagus officinalis* grows in the vicinity on a fixed sandy plain or on other places on back dunes.

Inside the small dunes on the sandy plain, occupied chiefly by the golf links, a grassland of varying structure is present. *Elymo*-*Ammophiletum* is just succeeded by *Violo*-*Corynephorum* as a consequence of an optimal sand burial. A well-developed typical subassociation can be seen with *Viola canina* var. *dunensis*, *Artemisia campestris*, *Hieracium umbellatum* ssp., *Festuca arenaria* and, in a few places *F. polesica*. A further succession leads to *Salici*-*Empetretum Polypodium vulgare* subass. Another *Galio*-*Koelerion* community is *Tortulo*-*Phleetum arenarii* in a small segment on the west side physiognomically determined by *Festuca* spp. and diagnosed by the presence of *Phleum arenarium*, *Sedum acre*, *Cerastium semidecandrum* coll. and *Tortula ruralis* var. *ruraliformis*. A few individuals of *Eryngium maritimum*, characteristic taxon of

Elymo-Ammophiletum, are present. The floristic structure shows agreements with a *Phleum arenarium* comm. (Raabe 1950) on the island of Fehmarn; see also a *Tortuleto-Phleetum arenarii* (Westhoff et al. 1962). Friesendahl (1926) has given an *Eryngium* ass. also of interest in this complex. A *Bromus hordeaceus* (ssp. *Thominii*) comm., rarely found on an inward beach ridge and probably corresponding to a *Festuco-Galietum maritimi*, constitutes a transition between *Galio-Koelerion* and *Thero-Airion* (see Westhoff et al. op.cit., Westhoff & Den Held 1969), the latter represented by an *Aira praecox* - *Armeria maritima* var. *elongata* comm. with *Rumex tenuifolius* and *Carex arenaria* on poor sand on the golf links, on the beach ridges physiognomically determined by *Corynephorus canescens* and *Festuca ovina*. In the later stage a transition towards *Spergulo-Corynephorion* is also possible and thus it becomes a part of *Cladonio-Corynephorum*. The difference in soil reaction between *Tortulo-Phleetum arenarii*, pH 6.5 (in KCl 5.9), and that of *Thero-Airion*, 4.6 (3.6), is obvious. To the picture of the very interesting gradients of *Koelerio-Corynephorum* at Falsterbo an *Erodium glutinosum* comm. on nearly naked soil, a *Festuca trachyphylla* - *Corynephorus canescens* comm. and a *Dianthus deltoides* comm. on less dry ground can be added.

Skanör's Ljung is a wet heath largely overgrown with *Ericion tetralicis* (Malmer et al. 1965, Rasmusson & Rasmusson 1970, Tyler et al. 1973) with a difficultly penetrable soil of marine sand and sea gravels (Holst 1895). A *Molinio-Myricetum* gale typical subass. is in some places surrounded and in normal succession replaced by *Myrico-Betuletum pubescentis* disturbed by drainings and pine plantations. *Quercus robur* is only sparsely found and confined to dry ground.

Sandhammaren

The sands marked as a foreland are estimated to include more than 1000 ha. The stretch of the coast line is about 15 km from Löderup Beach on the south coast to the fishing village of Skillinge on the east coast. In the central part near the lighthouse the distance landwards is about 1 km, much narrower in the peripheral parts. Löderup Beach, with many summer cottages, is situated outside the moraine esker of Kåsebergaåsen to the east in contact with the drained mire Hagestads mosse inside the area of

aeolian sand, near the seashore with pronounced dune rows. Within the dune landscape there are broken dune ridges, 10-15 m in height, in W-E direction, more complicated on the east side as a consequence of the situation at a corner. Between the drained mire, separated into two halves (see Nilsson, T. 1935 p. 465, Kurck 1917, Richter 1934-36, Davidsson 1963) by an elongated beach ridge, and the sands there are several beach ridges heaped up in places concealed by the aeolian sand forming a heath landscape, Järarna. The former sea bottom is in the soil profile marked with sea gravels (Moberg 1895). The dune landscape, Järarna and Hagestads mosse were included in the name 'Mälar' (Cronberg 1762) bordering on the arable land. In a dune system near the town of Ystad, separating a mire from a smooth bay, beach ridges are both concealed by aeolian sand and visible with sea gravels and small stones (see Holst 1902, Nilsson, T. op.cit. p. 458). In 1939/40 an area of 299 ha near the small river Tygeån at Sandhammaren was made into a reservation (see Dahlbeck 1940, Månsson 1960, Weimarck 1960). About 600 ha, including 270 ha coniferous and 80 ha deciduous forest, were investigated in 1970 (Olsson et al. 1971) with the idea of enlarging the nature reserve.

The beach SW of the lighthouse, strongly variable in width as a consequence of waves and winds, is normally plain with shallow moist hollows and miniature barchans. In certain years a luxuriant *Cakiletum maritimae* is present, also recorded by Warming (1909 p. 356), due to fluctuations in the tang supply, surrounded by *Elymo-Ammophiletum Salsola kali* variant. A *Loto-Trifolion* salt/fresh gradient community (Westhoff et al. 1962, Westhoff & Den Held 1969), diagnosed by *Lotus tenuis* and *Centaureum vulgare*, which occur together with *Rumex crispus*, *Agropyron repens* and *Potentilla anserina* with a green moss carpet including *Pohlia annotina*, inhabits several of the moist hollows. According to the colour of the tall dune grasses, *Elymo-Ammophiletum* forms three zones within the seaward dune rows, viz., a green one with embryo dunes dominated by robust tufts of separate clones of *Elymus arenarius*, *Ammophila x baltica* and to a lesser extent *Ammophila arenaria* where the sand contains drift materials rich in nutrients, a second yellow zone physiognomically determined by *Ammophila arenaria* and debilitated *A. x baltica* on a partly stabilized sand that *Petasites spurius* seems to



Fig. 37. *Salici-Empetretum* *Lophocolea heterophylla* subass., *Calluna* ring. In the central parts *Cladonia* spp. on dead heather. Sandhammaren 1970. Photo K. Jonsson.

prefer, and a third gray zone with *A. arenaria* of reduced vigour, the yellow flowering *Hieracium umbellatum* ssp. and the pioneer moss *Ceratodon purpureus* in the ground layer on fixed dunes. *Elymo-Ammophiletum* sometimes contains various mushrooms (see Andersson, O. 1950 a, 1950 b) and is an important habitat for many insects and spiders (see Ardö 1957, Almquist, S. 1969). In the lower parts between the dune rows *Corynephorus canescens* may be predominant. Moreover ruderal *Honkenya peploides*, less common on the beach, occurs.

On the final highest dune row, often the third, there is *Salici-Empetretum Polypodium vulgare* on the lee slope with less dwarf shrubs and with conspicuous cryptogams such as *Parmelia physodes* and *Dicranum scoparium*. Inwards just below the slope an initial dune depression seems to be formed, indicated by young *Betula verrucosa* and with *Salix arenaria* in the undergrowth. A fragmentary *Violo-Corynephoretum Cladonia* subass., also with some *Koelerion glaucae* plants such as *Koeleria glauca* and *Festuca polesica*, on instable sand due to an inward movement of the outer dunes, is in contact. *Koeleria glauca*, rather rare in the rest of the dune landscape, may occur in carpets of *Salix arenaria* as well as ruderaly in various tracks. The border between *Violo-Corynephoretum* and *Cladonio-Corynephoretum*, in some places may be difficult to draw as well as that between *Salici-Empetretum* and the inner *Calluna vulgaris* soc. The mosaic between *Cladonio-Corynephoretum* and the dwarf shrub heath is often recognized as *Calluna* rings on a lichen

ground. *Calluna vulgaris* settles in small 'islands', later advancing into successively growing rings. The centrifugal growth of *Calluna vulgaris* (see Watt 1955) is attributed to the fact that the heather makes the soil unfavourable for itself and thrives only in the peripheral rings, dying away in the central parts. The phenomenon may also be a result of allelopathy. *Calluna* rings have not been registered on the inland sands. Rings of *Juniperus communis* have been described by Wibeck (1906) from Slättö Sand in the province of Småland. Seedlings of *Calluna vulgaris* within the rings are normally absent. Instead *Empetrum nigrum* invades the destroyed spaces (see Böcher 1941 b p. 32, 1952 pp. 9-16).

At least in the seaward stands the dwarf shrub heath seems to be in equilibrium with a lichen vegetation composed mainly of *Cladonia* spp., sparsely also of *Parmelia physodes*, *Cetraria glauca* and *Usnea hirta*. It is interesting to notice that *Corynephorus canescens* is more vitalized in the border line between *Calluna vulgaris* and *Empetrum nigrum* than in the closed moss carpet where *Corynephorus canescens* is strongly debilitated. In degenerating *Calluna* with *Empetrum nigrum*, *Polypodium vulgare* occurs. Very pure patches of *Empetrum nigrum* are regarded a later stage in the regression, recognized in the surface soil as an increased organic layer. A settlement of *Quercus robur* and *Betula verrucosa* may occur as well as of ruderaly growing *Lathyrus maritimus*. It seems easier for *Calluna vulgaris* to recolonize on the *Empetrum* lawns than to advance on the lichen carpets; observed since 1965. *Salix arenaria* plays a



Fig. 38. *Melampyro- Quercetum roboris Calamagrostis epigeios* vicariant *Corynephorus canescens* subass. Oak clone consisting mainly of basal shoots. Sandhammaren 1970. Photo K. Jonsson.

more subordinate role, immigrating *Salici-Empetretum* from surrounding depressions. Sometimes *Salix arenaria* is high-growing also on dead heather. The regeneration of *Pinus sylvestris* and *Betula verrucosa* is more striking than that of *Quercus robor*. This is characteristic of *Salici-Empetretum Lophocolea heterophylla* subass., here in a zone after *Polypodium vulgare* subass., moreover in some dune valleys with preserved moistness favouring the vitality of *Calluna vulgaris*. In this complex a few relict mats of *Arctostaphylos uva-ursi* with scattered *Hypochoeris maculata* and *Campanula rotundifolia* may be mentioned.

The depressions behind the outer dunes are physiognomically determined by *Betula pubescens*, *Alnus glutinosa* subordinate often in a juvenile form. An exception is small stands near Mälarhusen where an *Alnus glutinosa - Typha latifolia* comm. is found (Olsson et al. 1971). *Myrica-Betuletum pubescentis* occurs very rarely with *Myrica gale* and *Vaccinium uliginosum*, near the small river Tygeån with a combination of *Myrica gale* and *Carex acuta*. *Polytricho-Betuletum pubescentis* is the main constituent of the depressions, on the driest parts transformed into *Melampyro- Quercetum roboris Betula verrucosa* var., which often borders on *Salici-Empetretum*. In a zone between the driest and wettest parts *Polytricho-Betuletum pubescentis Carex nigra* var. is obvious. A relatively open birch vegetation is described by Paul (1953 p. 308) from Kurischen Nehrung where *Agrostis canina* and *Calamagrostis canescens* are mixed with *Carex nigra*. In stands dominated by *Polytrichum commune* on the ground the

phanerophyte layer is more closed, often more than 80 %. *Caricetum canescentis -nigrae Carex canescens* soc. has occupied an earlier site of *Polytricho- Betuletum pubescentis* as several dead birches show. In still wetter habitats *Carex rostrata - Juncus effusus* comm. occurs.

In small isolated depressions the vegetation complex of *Caricetum canescentis -nigrae*, *Comaro-Salicetum auritae* (Passarge & Hofmann 1968), syn. *Frangulo- Salicetum auritae* (Westhoff & Den Held op.cit.), and *Polytricho-Betuletum pubescentis* has been studied. The first plant community is developed as *Sphagnum recurvum* subass. (see Warming 1914 pp. 336-337, Wangerin 1921) on places with a high water table during the whole vegetation period. *Comaro- Salicetum auritae*, surrounded or in a mosaic, is a dense to closed, double or triple-layered, nano-phanerophyte community dominated by *Salix aurita* accompanied by *Rhamnus frangula* and with sedges and *Sphagnum* spp., mainly *S. fimbriatum* in the undergrowth. In the very poor, acid depressions at Sandhammaren *Salix cinerea* is absent and found only in the drained mire, Hagestads mosse. The third component in the complex *Polytricho- Betuletum pubescentis* is more irregular in structure, with *Carex rostrata* and *Sphagnum fimbriatum* in lower parts separated by tussocks of *Polytrichum commune* and *Aulacomnium palustre* on higher ones. In certain moist hollows there is a pioneer *Polytrichum* comm., of a special kind by Warming (loc.cit.) named *Polytricheta* with *Polytrichum perigoniale* (in Nyholm 1954-69 *P. commune* var. *perigoniale*). It seems to correspond to a related vegetation

described by Wangerin (op.cit.) and Hueck (1932) from the opposite side of the Baltic.

In the inner dune landscape, largely occupied by oak- and pine forests, to a lesser degree by deflations and blow-outs, a *Calluna vulgaris* soc. is often in a mosaic with *Cladonio-Corynephoretum*, here more pronounced with *Cladonia dactylota*, rarely also *Cetraria islandica* but without *Stereocaulon condensatum* found at Furuboda. In the wind furrows with optimal sand burial a *Corynephorus canescens* soc. is established, also favoured in the border on pine stands. In *Calluna vulgaris* soc. the oak regeneration is obvious and the heather area has been strongly decreased (Dahlbom 1777/78, Olsson 1972 a) as a result of discontinued grazing. In shallow hollows in the dwarf shrub heath a *Molinia coerulea* soc., regarded a part of *Molinio-Myricetum gale*, is maintained, surrounded by a dead zone of *Calluna vulgaris* with scattered *Erica tetralix* and *Juncus squarrosus*. Adjacent moist *Calluna vulgaris* stands are high-growing with a badly developed moss layer contrary to dry, sun-exposed dune ridges, where *Cladonia* spp. included *C. rangiferina* are more predominant and *Calluna vulgaris* is somewhat lower. On extremely dry places just upon the ridges *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi* are relicts from an earlier epoch, rather free from forests, and they are possibly constituents of a heath corresponding to a final stage after a *Calluna-Cladonia* comm. (Böcher 1941 a p. 88) from inland sands on Jutland. On the north sides of the dune ridges *Vaccinium myrtillus* can be seen together with *Calluna vulgaris* on a thick moss mat of *Pleurozium schreberi* with sparse *Hylocomium splendens*. The podsolation is here pronounced and differs from the ranker soil of *Salici-Empetretum* more seawards.

Deschampsia flexuosa-*Pinus sylvestris* comm. is more frequent than *Vaccinio-Pinetum sylvestris* *Empetrum nigrum* subass. and *Cladonio-Pinetum sylvestris*. The first one is seen on light stands often bordering on *Calluna* rings, in the center with pine seedlings normally superseded by oak, besides a special phase on the seaward dunes with low trees on a closed *Empetrum nigrum* carpet corresponding to a part of *Empetro nigri-Pinetum* (Wojterski 1964 b Table 30). The coniferous lichen forest consists of a *Corynephorus canescens* subass. very irregular and fragmentary on open dry habitats and a typical *Cladonia rangiferina* subass. with a closed lichen carpet, only registered from two places. The podsol

is more obvious in *Deschampsia flexuosa* - *Pinus sylvestris* comm. compared with the other forests, in some stands also with a podsol-ranker.

On the dune ridges *Melampyro-Quercetum roboris* is low-growing and shrubby. The crooked bunches of trees (see Weimarck 1960, Olsson op.cit.), 5-7 m high form a closed canopy with *Convallaria majalis* and *Deschampsia flexuosa* in the undergrowth, sharply contrasting to adjacent heaths or eroded, naked sand. Secondary *Deschampsia flexuosa* may be replaced by *Corynephorus canescens*. The aspen imitates the oak in low degenerated stands where *Convallaria majalis* is replaced by *Maianthemum bifolium*, often with *Polypodium vulgare* present. In the open dune landscape *Quercus robur* is seen creeping, forming green carpets originated from *Calluna vulgaris* soc. The most extensive type of oak forest is *Luzula campestris* var. varying from shrubby to upright high stands. A few hummocks with *Leucobryum glaucum* and *Polytrichum formosum* occur very rarely. The acidophytes *Vaccinium myrtillus* and *Pteridium aquilinum* characterize the most podsolized variants, in the second with pan (see Benrath & Jonas 1937, Libbert 1940 p. 70). On moist ground the oak forest contains sparse *Molinia coerulea*, which is more associated with the birch forests except in the birch fen forest just inside the seaward dunes.

In the oak forest near the esker of Kåsebergaåsen on the west side of the small river Tygeån, the floristic structure is somewhat different, in *Melampyro-Quercetum roboris* *Corylus avellana* subass. the field and bottom layers are reduced. One *Peucedanum oreoselinum* var. is marked by the oaks obvious in bunches. In a margin vegetation *Agrostio-Quercetum roboris* is found just below the slope of the esker, covered by a deciduous forest belonging to *Peucedano-Quercetea* (Passarge & Hofmann 1968) on instable soil and with various termophytes such as *Cynanchum vincetoxicum* and *Lonicera xylosteum*.

Near the outlet of the small river there is a *Salicetum arenariae*, both *Ammophila arenaria* subass. and *Carex nigra* subass., in the latter with *Hypochoeris maculata* and *Potentilla erecta*. Upstream the river is edged by plants from *Phragmitea* as well as tall shrubs of *Salix* spp. A closed distinct *Calamagrostis epigeios* comm. is found. Along a road parallel to the river nitrophilic tall shrubs belonging to *Urtico-Sambucetea* are seen



Fig. 39. Planted *Pinus mugo*. Sandhammaren 1970. Photo K. Jonsson.

(see Jessen 1968 Table 26), especially *Sambucus nigra* as well as adjacent *Prunus spinosa* shrubs of *Prunetalia spinosae* (Blomquist 1911, Tüxen 1952).

A large part of the pine plantation on the heath Järarna seems to correspond to a *Galio-Pseudopinetum* (Passarge 1962 b) with *Lonicera periclymenum* and *Galium saxatile*, a NW vicariant of *Scleropodio-Pseudopinetum* (Hofmann 1964). In some stands *Dryopteris austriaca* is frequent.

Vitemölla

The East Scanian coast is composed mainly of sand. The slopes of Vitemölla and the Ravlunda field constitute a glacifluvial formation. Landwards from Juleboda the glacifluvial sand reaches its maximum and extends about 3 km. Just south of the gneiss rocks of Stenshuvud there is another glacifluvial field, also with a sharp border to the beach (see Andersson, E. & Nilsson, J. 1971).

The slopes of Vitemölla are situated between the fishing village and the small river Verkeån. Below the steep slopes there is a plain composed of both glacifluvial material and aeolian sand, sharply edging the outer fragmentary dunes inhabited by *Elymo-Ammophiletum* with frequent *Lathyrus maritimus* and in some places with *Eryngium maritimum* and *Petasites spurius*. On the small beach the drift vegetation is reduced or absent. The zonation in a transection landwards has been studied by Erikson (1896) and Sernander (1919), who made a division into the beach, the dunes and the sandy fields. Sernander (1925) introduced the supralittoral, epilittoral and supramarine zones above the littoral and Ardö (1957 p. 90) used the terms fore shore, high shore, fore dune, dune ridge and dune heath. According to

Sernander (1925) a *Triticum junceum* -ass. is replaced by a *Psamma*-ass. and in later stages a *Festuca sabulosa*-ass. and a *Corynephorus-Rhacomitrium*-ass. corresponding to *Violo-Corynephorum* favoured by weak sand burial in the typical subassociation, otherwise marked as a *Cladonia* subass., and a *Thymus serpyllum* - *Festuca polesica* -ass. respectively in the Baltic region (see Regel 1928). On the foot of the hill slope a meadow vegetation with *Scabiosa columbaria*, *Knautia arvensis*, *Geranium molle*, *Carex hirta* and *Dactylis glomerata* is mixed with plants from *Festuco-Sedetalia* such as *Trifolium arvense* and *Armeria maritima* var. *elongata*.

On the calcareous slope as well as on parts of the top of the hill *Antherico-Koelerietum glaucae* occurs (Stern 1922, Andersson, O. 1950 a, Tüxen 1951, Ljungberg & Persson, Y. 1973), the typical subassociation with a striking moss layer and a *Cladonia* subass. where the soil is more leached. In dry sun-exposed habitats *Anthericum liliago* is present. An increased rabbit population is through burrowing of importance for maintaining *Antherico-Koelerietum glaucae*, which is weak in competition. Just below the pine plantation there is probably a fragment of a *Tortulo-Phleetum arenarii* (see Westhoff & Den Held 1969, Hallberg 1971) on very instable glacifluvial soil. Patches of dry-growing *Elymus arenarius* are seen on the slope but they are not similar to a *Berteroa incana* - *Elymus arenarius* comm. near the village of Kivik. A dry meadow vegetation (see Böcher 1945, Andersson, O. 1950 a) is found on the seaward sides of the steep hill of Haväng.

The pine plantation (see Ljungberg & Persson, Y. op.cit.) above the sands of Vitemölla has agreements with a grassy *Pinetum herbidum* (Sernander 1920) in some places with relicts of *Anthericum liliago* and *Scabiosa canescens*. As Areschoug (1866) and Sernander (loc.cit.) have pointed out the East Scanian sands are unique and parts had to be preserved from total afforestation. Though there are relationships to an eastern *Peucedano-Pinetum* (Matuszkiewicz 1962) found on the island of Öland (Sterner 1926 p. 125) and that of Gotland (Du Rietz, G.E. 1925 d, Pettersson 1958 pp. 33-34) the forest may in East Scania be regarded a *Pseudopinetum*.

Furuboda

On the bay Hanöbukten a dune landscape is situated between the small river Julebodaån bordering on the Ravlunda field in the south and the village of Åhus in the north. Between the two outlets of the river Helgeån and just south of the Furuboda area, the sands reach maximal dimensions. A drained lagoon mire (Nilsson, K. 1966 Plate 6) occurs parallel to the maritime sands and is replaced landwards by a broad zone of inland sand, earlier very rich in species (see Linné 1749, Erikson 1896) now cultivated or afforested. The outer dune ridges parallel to the shore line are somewhat broken as well as the inner dune ridges, also formed as parabola dunes with central parts displaced to the sea (Bergstedt 1931). The highest dunes are about 25 m surrounded by blowouts and hollows. De Geer (1889) and Bergstedt (op.cit.) have reported deflations with sea gravels, also seen at Haverdal.

On the narrow beach the halophytes are nearly absent. A small fringe of *Elymo-Ammophiletum*, rarely with *Eryngium maritimum*, covers the fore dunes and is succeeded inwards by *Violo-Corynephorretum* rich in *Carex arenaria*. The pronounced dune row has *Ammophila arenaria* soc. On lee slopes also perpendicular to the shore line *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass. occurs, often in contact with an *Agrostis tenuis* - *Populus tremula* comm. with various nano-phanerophytes (see Erikson 1896). Compared with related stands at the west coast the present tall shrubs are less streamlined by the wind action. In the vicinity *Cladonio-Pinetum sylvestris Corynephorus canescens* subass. appears in shrubby stands with relicts from surrounded vegetation such as *Elymo-Ammophiletum* and *Cladonio-Corynephorretum*. The



Fig. 40. *Carex arenaria* runners. Furuboda 1954. Photo H. Weimarck, Skånes Naturskyddsför. Arkiv.

latter one is situated on the inside sandy plain, where patches of *Corynephorus canescens* in open stands are in a mosaic with *Carex arenaria* in closed stands as well as with the naked sand. These two phases represent stages in a cycle on the sand controlled by the wind. Thus *Corynephorus canescens* soc. or typical subassociation is formed at optimal sand accretion and *Cladonia* subass. with abundant *Carex arenaria* when the sand burial has ceased. The latter is often developed as a *Cetraria crispa* var. making the ground dark in colour. Of special interest is a stand with *Cladonia dstricta* and *Stereocaulon condensatum*, on the island of Gotska Sandön only the latter (Arwidsson 1938), adjacent to stands rich in *Cladonia arbuscula et mitis*. A reversible change between *C. dstricta* and *C. mitis*, as given by Böcher (1941 b p. 19), has not been registered. At Furuboda Agrell (1934) has studied a microecosystem of a *Collembola* sp., *Xenylla maritima*, in maximal frequency inhabiting a tuft of *Cladonia* spp.

Rarely small cushions of *Salici-Empetretum Polypodium vulgare* subass., with *Empetrum nigrum*, *Polypodium vulgare*, *Parmelia physodes* and *Pleurozium schreberi*, occur on the sandy plain. Another plain further to the north contains some hummocks of *Salicetum arenariae* *Ammophila arenaria* subass. extremely rare on the dunes. Below solitary pines there are *Cladonia* spp., also *C. impepa* and *C. crispata*, peripherally surrounded by a

ring of *Salix arenaria*, which according to Hultén (1971) is uncommon in the coastal districts of the province of Blekinge not far from Furuboda.

On the seaward slope of a second high dune row, inland from a *Cladonio-Corynephoretum* there is a mosaic with *Cladonio-Pinetum sylvestris* *Corynephorus canescens* subass. On stable sand behind the dune row a typical subassociation, besides *Cladonia rangiferina* also with the boreal *C. alpestris*, in a very closed lichen carpet, has been seen on one small site. Upon and just behind on the leeward slope a *Deschampsia flexuosa* - *Pinus sylvestris* comm. is transformed into a *Vaccinio-Pinetum sylvestris* *Empetrum nigrum* subass. with *Vaccinium* spp. and a well-developed moss layer. A fragmentary *Pyrolo-Pinetum sylvestris* (see Tüxen 1951 p. 164) in the vicinity at Espet near Åhus. is an indication that the original forest here was of pine, not oak. Also the presence of *Cladonia alpestris* agrees with this hypothesis. Lindblom (1782) reported various pine forests with trees ready for felling on the sands lacking any oaks.

INLAND SANDS

Ålstorp

The sands between the villages Löddeköpinge and Saxtorp in West Scania are composed of a mixture of glacialfluvial and aeolian sand, partly covering the drained mire, Hosterups mosse. The dirty-coloured sand is not clean but mixed with a powder of both mineral and organic origin (Erdmann 1881 p. 34). A large part of the area is afforested, cultivated, utilized as sand-pits and exploited for summer cottages. *Teesdalia-Corynephoretum* *Artemisia campestris* subass. with much *Helichrysum arenarium* is predominant on open places, near a main road, physiognomically determined by *Hieracium pilosella*. A meadow vegetation of *Arrhenatherion elatioris* is adjacent. In an abandoned sand-pit *Anthyllis vulneraria* is abundant in certain closed stands, *Trifolium arvense* and *Oenothera biennis* in other more open ones. Moreover, a pioneer community with *Herniaria glabra*, *Ononis repens*, *Erigeron canadense* and *Senecio vernalis* is registered. Near a *Pseudopinetum* with *Agrostis tenuis* in the undergrowth there is a new sand-pit with rapidly colonizing plants. Small tufts of *Corynephorus canescens* can in some places be seen on a bare ground. On a wall with cast up surface soil is a luxuriant ruderal vegetation.

Flyinge

Near the village of Flyinge there is a sandy hill, in the central parts with a wide deflation originating from an earlier sand-pit. On the naked sand an open *Teesdalia-Corynephoretum* is present with solid tufts of *Corynephorus canescens*, here more robust than on the coast, as well as dispersed pioneers, such as *Senecio vernalis* and *Cerastium semidecandrum*. In a wind furrow the vitality of the plants is favoured due to continuous sand burial. On the hills a closed grassland occurs with patches of *Agrostio-Callunetum*, partly overgrown by *Agrostis tenuis* and other grasses.

Revingehed

Near the military base there is a sandy hill, one of several, in the direction towards the village of Silvåkra. The configuration is a result of a wide sandy delta. High sand dunes are absent (Ekström 1961 p. 22). The poor outwashed sand characterizes the soil of a *Calluna vulgaris* soc. with a bottom layer of *Cladonia* spp. An analyzed *Teesdalia-Corynephoretum* on the edge of the hill has certain agreements with *Cladonio-Corynephoretum*. On a slope an *Agrostio-Quercetum roboris* with a tendency to bunch formation is seen, on the lowest part bordering on *Myrico-Betuletum pubescentis*, marked with various graminids such as *Calamagrostis canescens* and *Molinia coerulea*. In a moist habitat in the vicinity there is a swamp vegetation. Along the main road a *Pseudopinetum* is characterized by the presence of *Rubus idaeus* and *Impatiens parviflora* on a dense mat of *Deschampsia flexuosa*.

Silvåkra

On the field used for military training, at the confluence of the rivers Klingaälvån and Kävlingeån, there is a sandy grassland belonging mainly to *Teesdalia-Corynephoretum*. A typical subassociation, well developed with rapidly growing *Corynephorus canescens* and *Teesdalia nudicaulis* on the naked sand, could not exist without the wear and tear from military vehicles. *Artemisia campestris* subass. grows in some places with an abundance of *Carex arenaria*. Heather initials are seen. In one stand the combination of *Agrostis canina* ssp. *montana* and *Filago minima* is striking. The anthropogenous *Berteroa incana* - *Elymus arenarius* comm. is distributed near the river but also in

patches inwards on the field joining *Anchusa arvensis*.

Vomb

Linné (1749) observed that the Vomb plain was the poorest in Scania with *Rumex tenuifolius*, lichens and heather in the fallows. Hallenborg (ca. 1750) was of the opinion that the fields originated from a forest and were a result of a primitive cultivation. The grassy fields on glaciuvial sand have periodically been used as arable land (Sernander 1915 p. 451). Munthe et al. (1920 p. 140) have reported dune rows 5-8 m in height composed of both aeolian and glaciuvial sand. In the wide afforestation, Vomb's Fure, with a *Deschampsia flexuosa* - *Pinus sylvestris* comm., *Galio-Pseudopinetum* (see Køie 1938 Table 9:12-13, Passarge 1962 b) and larch stands, there is an elongated dune.

Near the small village of Vomb the soil consists of a rather coarse, dry sand, poor in organic matter (see Ekström loc.cit.). *Teesdalia-Corynephorum* is rich in *Cladonia glauca*, in some places with *Euphorbia cyparissias* moreover a component of an adjacent low-growing *Agrostio-Callunetum* near a *Pseudopinetum* with a dense field layer of *Carex arenaria*. The grazed grassland in the surroundings has several small denuded areas in the plant cover.

Björka

A sandy hill following the winding small river Björkaån consists of a rich differentiated vegetation. In small open spaces on the hill *Teesdalia-Corynephorum* characterized by many cryptogams, also the very rare *Cladonia elongata*, is surrounded by closed stands of *Festuca ovina*, *Hieracium pilosella* with scattered *Armeria maritima* var. *elongata* as well as a robust *Agrostio-Callunetum* with scattered pine seedlings immigrated from an afforestation in the vicinity. *Teesdalia nudicaulis* common in the sandy grassland grows, according to Weimarck (1940 p. 177, 185), in a zone corresponding to the water level of the ice lake, where sand and gravels have been deposited, as seen in the whole Vomb plain. Between a small road and *Agrostio-Callunetum* there is a poor meadow vegetation, *Rumex acetosa* - *Festuca ovina* comm. On the opposite side of the road a park landscape of *Agrostio-Quercetum roboris* with beeches, which are more typical on a slope with *Poa nemoralis* near the river, is found. A neighbouring coniferous forest, Björka

Fure, on a wide sandy plain consists of *Deschampsia flexuosa* - *Pinus sylvestris* comm., various *Pseudopinetum* and probably in old stands an established *Vaccinio-Pinetum sylvestris*.

Hemmestorp

On the east foot of the hill Romeleåsen several sand hills extend between the villages Sövde and Veberöd, partly cultivated with rye and potatoes, also utilized for sand-pits or exploited for summer cottages. A well-developed *Teesdalia-Corynephorum* (see Larsson, A. 1971) distinguishes the sands, often with *Rumex tenuifolius* and rarely *Arnoseris minima*, a relict from the rye fallows. A typical subassociation with *Polytrichum piliferum* near a sand-pit seems to be favoured by a continuous dust supply. An *Artemisia campestris* subass. is rich in *Hieracium pilosella* and *Hypochoeris radicata*. In a restored sand-pit pioneer community with *Senecio vernalis*, *Agrostis tenuis* and *Holcus mollis* is found. An *Agrostio-Callunetum* is situated between a *Pseudopinetum* and *Agrostio-Quercetum roboris*, further in contact with *Deschampsia flexuosa* - *Pinus sylvestris* comm. in which the oak has invaded; it is also seen at Sandhammaren.

Vitaby

On a glaciuvial hill between the small villages of Vitaby and Vitemölla the changes on old fallows may be studied. In a young stage of *Teesdalia-Corynephorum* a combination of *Agrostis tenuis* and *Corynephorus canescens* is obvious. In old stands *Agrostis canina* ssp. *montana* and *Polytrichum piliferum* are present, in some places also *Hieracium pilosella*. Near Haväng a rye field is situated near a *Rumex tenuifolius* fallow, the very first stage later overgrown with *Teesdalia-Corynephorum*. At Maglehem this stage is rich in *Aira praecox*, *Filago minima* and *Helichrysum arenarium* (Erikson 1896, Andersson, O. 1950 a), at Brösarp in contact with *Antherico-Koelerietum glaucae* (Mattiasson 1970, 1971), developed into an *Agrostio-Callunetum* with a podsol-ranker. On the ridge Linderödsåsen Linnermark (1966 Fig. 14) has reported a *Genisto-Callunetum* on a very pronounced podsol. At Vitaby oak immigrates into the dwarf shrub vegetation. On other places pine immigrates from adjacent afforestations, and is now widely distributed in east Scania. Tidström (1756 p. 59) had difficulties in saying where the woodlands began.

An ecological comparison of two dune systems

Methods

Sampling

Most of the samples were taken in 1966–67, but samples used for total soil mineral analyses in 1969–70. The soil samples were collected with a steel cylinder of known volume and a length of 10 cm, in a few cases 5 cm, from the levels 0–10, 20–30, 50–60 and 90–100 cm. Surface litter was avoided. All holes, dug in the sand, had a small diameter and from the deeper layers the samples were taken with special tools. Field percolation was performed with the use of cylinders, 40 cm in height and 8 cm in diameter, pushed down into the soil about 15 cm. The time required for half a litre of sea water to percolate was registered. Grain size and porosity were determined on sand from a depth of 50–60 cm. The grain sizes were obtained by sifting. The finest soil fractions constitute only a very small part and were disregarded. The density of dry sand must be mentioned to get information of the material volume. Air and water volumes are calculated on the basis of the water content, determined by drying at 105°C.

The volume weight is the relation of fresh soil weight to the cylinder volume. It must be known for all calculations on volume basis. In sandy soils it is ca. 1.5, in organic layers much lower. The samples were homogenized through a 2 mm sieve. In certain cases a correction was made for roots.

The loss on ignition was obtained after heating to 600°C of the dried samples. It has been expressed as percent in earlier chapter of this work; in this chapter it is expressed as g/dm³ or kg/dm³, as this is more suitable for comparison with other parameters in the various ecosystems. The pH was determined in a soil suspension or directly in the water samples (see earlier chapter). Available mineral constituents were determined in 0.5 M HAc (acetic acid), which is suitable for sandy soils (see Wright 1956 p. 34). A sample of 50 g was extracted in 150 ml 0.5 M HAc for three hours and afterwards filtered.

Plant samples were cut from 1 m² squares including both above ground living and dead material. Plant samples were collected less frequently than soil samples, four times and seven times respectively. Water samples were taken from the sea, the dune depressions and the small river Genevadsån at Tönnersa.

Soil analyses

Na and K were analysed with the aid of an EEL flame spectrophotometer. Ca and Mg with a Perkin-Elmer atomic absorption spectrophotometer. Cl was determined by a mercurimetric method with diphenylcarbazone as indicator (see Clarke 1950 pp. 553–555, Goldman 1957 p. 1127). The method allows very low concentrations of Cl in the titration. According to Clarke (loc.cit.) a mixed indicator is used in the pH-interval 3.0–3.5. No contaminations influenced the results. Goldman (loc.cit.) adjusted the pH to ca. 2.5 with the aid of a second indicator, xylene-cyanol FF. The method was modified in the following way by the present author: 25 ml extract are acidified with 2 drops of concentrated HNO₃; about 1 ml of the latter indicator (1 g in 50 ml 95 % alcohol) is added, giving a pH of ca. 2. The amount of indicator can be successively diminished at higher Cl-concentration. Several blank titrations must be made.

S was determined by a turbidimetric method (Chesnin & Yien 1950 pp. 149–151, Bardsley & Lancaster 1960 pp. 265–268, Blanchar et al. 1965 pp. 71–72). According to Rossum & Villaruz (1961 pp. 873–876) the method is rapid, effective and has high sensibility. Active carbon may be used in contaminated extracts, sometimes resulting, however, in reduced S concentrations. In extracts from pure sand there were no differences. To obtain as high precision as possible Fox et al. (1964 pp. 243–246) have suggested digestion of the samples prior to determination. The present author has modified the method in the following way: 20 ml extract are supplied with 1 ml of an 'acid-seed' sulphate solution (20 ppm S in 1:1 HCl). With a standard cup about

1 g BaCl₂ is added. The crystals are 0.2–0.6 mm in diameter. Together with a small amount of gum arabic the solution is gently shaken for exactly 30 seconds. 5–30 minutes later the extinction due to turbulence is measured with a Unicam spectrophotometer.

P was determined by the usual molybdate method (Trouw & Meyer 1929 p. 137, Williams & Stewart 1941 pp. 291–297, Ginzburg 1956 pp. 169–178, Chang & Jackson 1957 pp. 133–144). According to Williams & Stewart (op.cit.) it is important that the molybdate concentration is 2.5 % and the sulphuric acid 5 M in the initial solution. A final solution may contain 0.1 % and 0.2 M respectively plus 0.008 % SnCl₂. The method is a 'direct method' with high accuracy (Williams & Stewart op.cit.). Ginzburg (op.cit.) has recommended P determination in various acid extracts, e.g., 0.5 M HAc, without digestion. The extinction was measured with an EEL colorimeter.

A HF-digestion (Pavluk 1967) was used to destroy SiO₂ and silicates in order to obtain the total amount of other soil mineral elements. Besides Ca, Mg, Na, K, S and P also Fe, Mn, Ti and Al were determined. Fe and Mn were analysed with the aid of a Perkin-Elmer atomic absorption spectrophotometer. Ti was determined according to Askund et al. (1966). The extinction of an orange-yellow Ti-compound in phosphoric acid was measured with a Unicam spectrophotometer. Some measurements on a Ti-complex with sulphosalicylic acid (see Schlichting & Blume 1966) were also made. Al was determined colorimetrically (see Schlichting & Blume op.cit.).

Plant and water analyses

The plant samples, representing the standing crop (see chapter Plant cover), included foliar samples as well as litter and putrified tang (seaweed).

The dry weight was determined after drying finally at 85°C for at least one day. Afterwards the plant material was ground. One gram of the ground samples was used in the analysis, and in addition, 0.1 g for the N determination. The analyses were performed in duplicates. The digestion followed a method proposed by Johnson & Ulrich (1960 pp. 25–78). It was started with HNO₃. Afterwards HClO₄ was added. After evaporation remaining sand grains (in the lichen-rich samples) had to be removed through filtration. The sand on the filter

was dried and weighed, and its weight subtracted from the initial weight of these samples.

All metals were analysed as described above. Ca was determined in a La-solution to minimize disturbances from anions. A 100 % recovery of S was never obtained but nearly so, if Ca:S was at least 1.5 :1 (see Shaw 1959 pp. 843–847). P was determined by a PVM-method (Rauterberg 1951 p. 149, Egnér et al. 1960 pp. 200–215). The extinction was measured with a Unicam spectrophotometer.

Cl was analysed in water extracts.

Total N was determined by the common Kjeldahl-method. A mixture of sulphates of K, Cu and Hg was used as a catalyst. Some soil samples were analysed both for total N and NH₄-N (see Black et al. 1965 pp. 1179–1237), the latter constituent after distillation and nesslerization.

The water analyses were made directly on untreated samples or in certain cases after filtration. The mineral components were determined as described above.

The reliability in field sampling and the analyses

The standard deviation in the field sampling is reported in the Tables 4, 5 and 9 and illustrated in the Figs. 56–77. These deviations are to a large extent due to the seasonal variation within the sites. To estimate the variation due to sampling and processing 30 duplicates from different sample series have been investigated. The results are reported below in the section Introduction to the determined parameters. The standard deviation was calculated with a confidence interval of 95 % according to the formula $\pm t \cdot s/\sqrt{n}$ (see Bishop 1968).

Soil

The soil profile

The naked beach as well as Honkenyetum peploidis contain some humus lenses, more pronounced at Tönnersa than at Sandhammaren. In Elymo-Ammophiletum Salsola kali var. the root system sharply borders an H₂S-layer. Humus lenses and root layers (see Salisbury 1952 p. 198) are common in Elymo-Ammophiletum typical subassociation. The rhizomes extend deeper than 100 cm. In some stands the dry surface soil consists of old basal shoots. Elymo-Ammophiletum Hieracium spp. subass. has often a thin moss-layer. Root layers and

Table 4. Porosity (%) and grain size (%). Average from 8 stands at the depth of 50–60 cm.

locality; stand no.	material volume	pore volume	air volume	water volume	grain size, mm			
					2.0–0.6	0.6–0.2	0.2–0.06	<0.06
Tönnersa; 1–6, 8–9	61±0.6	39±0.6	36±0.8	3.2±0.9	6.4	75±19	19±18	<0.1
Sandhammaren; 1–7, 9	58±0.9	42±0.9	36±4.2	6.2±3.9	<0.1	66±11	34±11	0.1

humus lenses could be found to a depth of 50 cm.

In some places at Tönnersa *Violo-Corynephorum* *Cladonia* subass. has a closed mat of lichens on a rather thick dark humus horizon, rich in fine and very fine roots. In the subsoil the sand is reddish and roots are almost lacking. At Sandhammaren the lichen crust is more openly situated on the sand, which is mixed with greyish humus and many small roots. The *Cladonia* (dstrictae) -*Corynephorum* investigated at Sandhammaren, both on denuded sites and on plains with a closed lichen cover, is often marked with somewhat darker humus in the surface soil where very fine roots alternate with solitary *Carex arenaria* roots. In the subsoil the sand is yellowish and almost free from roots.

Salicetum arenariae *Ammophila arenaria* subass. is in several stands rich in leaf litter on the surface. Humus lenses were found to a depth of about 50 cm. Scattered big roots extend deeper. In *Salicetum arenariae* *Carex nigra* subass. there are also some humus lenses (see Ranwell 1959 p. 588) and big roots. The depth of the latter is limited by the fluctuating water table. Sand accretion has led to irregularities in the soil stratification of *Salici-Empetretum Festuca arenaria* subass. The amount of humus is less in the surface soil than in the subsoil at 50 cm, where also a distinct root layer occurs. Only solitary roots extend deeper. A raw humus is formed in *Salici-Empetretum Lophocolea heterophylla* subass. The root system of the nanochamaephytes is shallow and concentrated to the O- and A-layers. In the latter the sand is mixed with dark humus. At Tönnersa, the small river Genevadsån in the neighbourhood has produced a high soil moisture at the depth of one metre or more.

Inland from the beach the organic layers in the surface soil have increased in thickness. The raw humus is less marked in *Salici-Empetretum Lophocolea heterophylla* subass. than in *Calluna vulgaris* soc., where the soil profile is a podsol. The most obvious podsol is found in various pine stands.

In the oak forest besides a podsol more rarely also a podsoloid may be developed (see earlier chapter).

Porosity and grain size

Sandy soils have a single-grain structure as a result of the weak cohesion between the soil particles. Adhesion occurs only in moist sand (Berger-Landefeldt & Sukopp 1965 p. 48). The porosity was 35–45 % (see Ovington 1950 p. 313), which may be compared with 40–60 % or more in aggregated soils. The average porosity was somewhat higher at Sandhammaren (42 %) than at Tönnersa (39 %) (Table 4). The air volume was about the same, 36 %, on the two localities, and highest in *Elymco-Ammophiletum* typical subass. The water volume was small but somewhat greater at Sandhammaren.

The main grain sizes were fine sand (0.2–0.06 mm) and coarse sand (0.6–0.2 mm). At Tönnersa the average amount of fine sand was 19 % and coarse sand 75 %, at Sandhammaren 34 % and 66 % respectively (Table 4). At Tönnersa there was about 6 % of very coarse sand (2.0–0.6 mm), generally found on the beach. On the beach bar in the northern part the fraction of fine sand was higher and the fraction of coarse sand smaller compared with the condition in the southern part. On the beach and most seaward dunes at Sandhammaren there was three times as much coarse sand as there was fine sand. Inland from the seaward dunes the proportions of the two fractions was more equal.

Field percolation

Some experiments with field percolation in various stands at the two localities were performed. Investigated segments were percolated at six places. The mean time was calculated and for the first experiment called 'dry' (Figs. 41–42). The percolation was repeated in the moist sand using the same cylinder holes. The new mean time was called 'moist' (Figs. 41–42). The time of percolation had changed due to the increase in soil moisture.

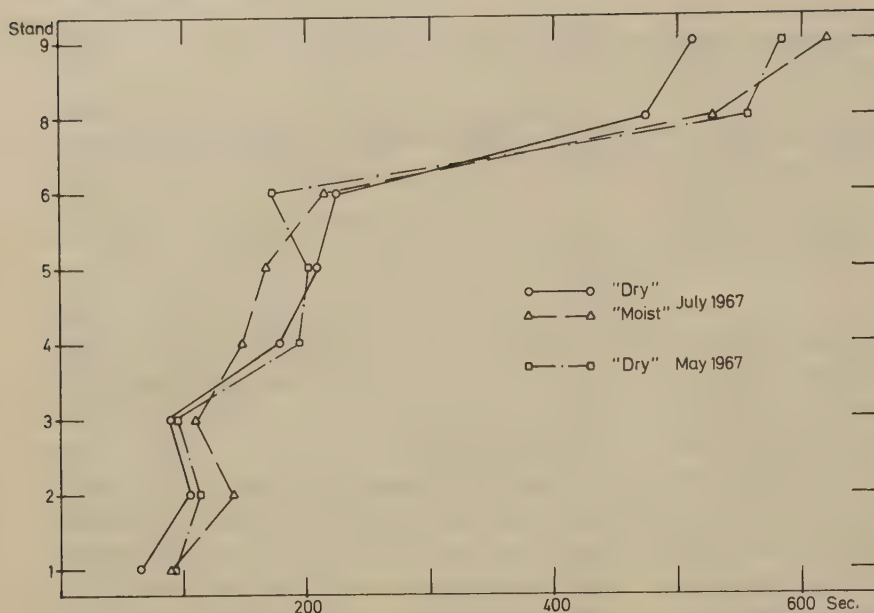


Fig. 41. Tönnersa. Field percolation (time for infiltration in various stands). "Dry" = percolated for the first time. "Moist" = percolated for the second time. The stands 1-6 and 8-9, see Fig. 43.

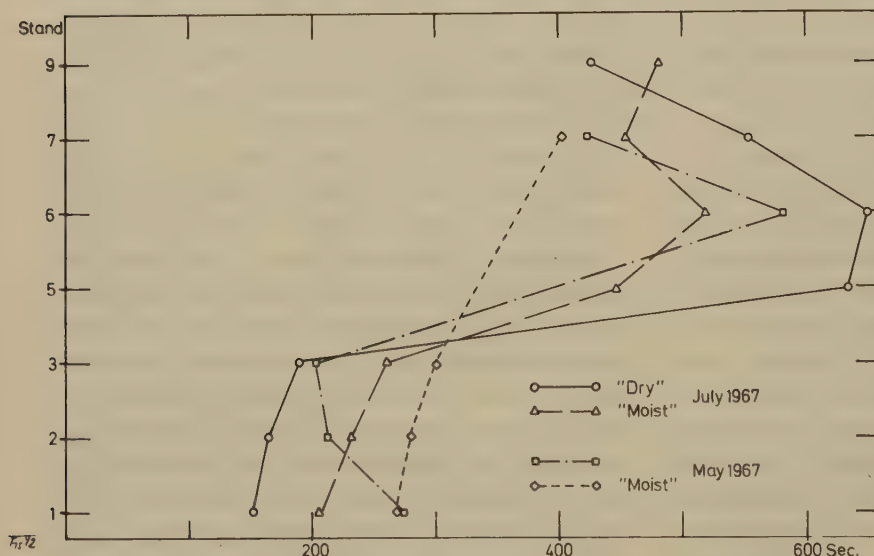


Fig. 42. Sandhammaren. Field percolation (time for infiltration in various stands). "Dry" = percolated for the first time. "Moist" = percolated for the second time. The stands 1-3, 5-7, and 9, see Fig. 44.

As seen in Fig. 41 the curve for May agrees with that for July. At Sandhammaren the curves are more separated (Fig. 42). At Tönnersa the diagram shows a rather small change from the naked beach (1) to *Salicetum arenariae* *Ammophila arenaria* subass. (6) (100–200 sec.). At Sandhammaren the percolation time was 150–300 sec., from the naked beach (1) to *Elymo-Ammophiletum* typical subass. (3). Further landwards the curve forms a peak in the stands of *Elymo-Ammophiletum* *Hieracium umbellatum* ssp. subass. (5), *Violo-Corynephoretum* *Cladonia* subass. (6) and *Cladonio-Corynephoretum* (7), with increased time of percolation (500–650 sec.). The peak

is a result of the difficult infiltration. The percolation was here more rapid the second time with reduced surface tension in the soil ('moist' curve). In the pure seaward sand as well as in the humus-rich *Salici-Empetretum* the percolation was more rapid the first time ('dry' curve). In *Salici-Empetretum* at Tönnersa (stands 8–9) the water had penetrated the soil after 500–600 sec., at Sandhammaren (stand 9) after 400–500 sec.

Introduction to determined parameters

The water table is high in the dune depressions, where the sand is moist and stable. It rises in winter

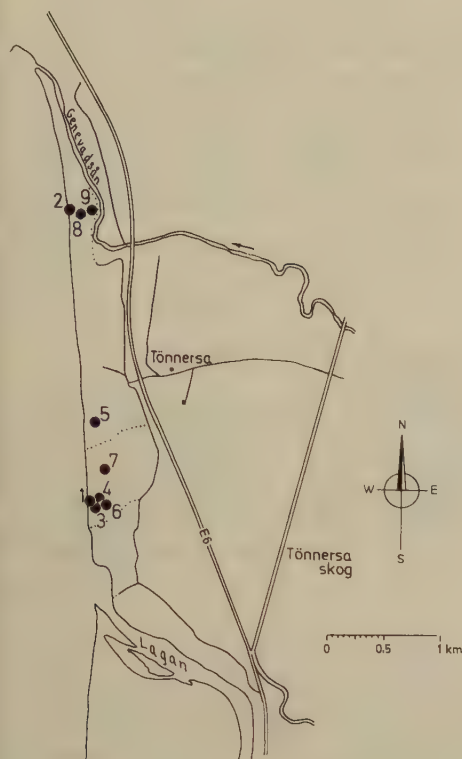


Fig. 43. Tönnersa. Location of the stands 1-9: (1) Naked beach; (2) *Honkenyetum peploidis*; (3) *Elymo-Ammophiletum* typical subass.; (4) *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass.; (5) *Violo-Corynephorretum Cladonia* subass.; (6) *Salicetum arenariae Ammophila arenaria* subass.; (7) *Salicetum arinariae Carex nigra* subass.; (8) *Salici-Empetretum Festuca arenaria* subass.; (9) *Salici-Empetretum Lophocolea heterophylla* subass.

and is lowered in spring and summer. In the autumn, when the precipitation is high and the evapotranspiration is low, the soil water content increases. A second type of influence is inundation of the beach and dune depressions. Also the sand movement affects the soil water. The diurnal rhythm of the vegetation and the age of the dunes are also of interest in this context.

In the non-calcareous dunes in South Sweden it is not necessary to make a correction for carbonates (see Gorham 1958 p. 375, Ranwell 1959 p. 589) when determining the organic matter as loss on ignition. The decomposition of the organic matter occurs more rapidly in calcareous soils than in siliceous soils. Under acid conditions accumulation is favoured. *Calluna vulgaris* by its litter accelerates humus accumulation also by slow decomposition (see Salisbury 1952 p. 301). When the air volume is strongly reduced, as in certain dune depressions, the



Fig. 44. Sandhammaren. Location of the stands 1-9: (1) Naked beach; (2) *Elymo-Ammophiletum* typical subass. *Salsola kali* ssp. *kali* var.; (3) and (4) *Elymo-Ammophiletum* typical subass.; (5) *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass.; (6) *Violo-Corynephorretum Cladonia* subass.; (7) and (8) *Cladonio-Corynephorretum Cladonia* subass.; (9) *Salici-Empetretum Lophocolea heterophylla* subass.

humus will be dark. There is in many cases a correlation between soil reaction and organic matter; for example, Holmen (1964 p. 144) showed a good correlation between pH and ash content in certain peats. In the seaward dunes the organic matter was low and the pH was high. Inland from the beach there was an increase of the humus and a decrease of pH. Wilson (1960 p. 355) has compared the gradual increase of humus, Olson, J. (1958 p. 159) the N content in surface soils with the age of the dunes.

The pH is only an approximative value in a soil suspension. The dilution has comparatively little effect on pH, which in KCl is about one unit lower than in H₂O. The layers O_h and A_h are very acid. On the sands very low pH values are registered from the pine forests. In the inner maritime dunes excess of sulphuric acid might control the pH (compare Gorham 1958 p. 78, and much recent literature on air pollution). Carbon dioxide from the micro-organisms, root exudates and various organic acids, formed in the soil, influence the leaching process (Wilson loc.cit.) in the sand. Moreover nutrient uptake by the vegetation (Jenny & Overstreet 1939 pp. 257-272) acidifies the soil. Also the competition between different plants is of importance. *Calluna vulgaris* normally grows at pH ca. 4 but occurs even at pH ca. 8 (Poelt in Stålfelt 1965 p. 304). The pH may be correlated to the type and amount of organic matter, the acid-base status and the Ca-content. The relationship between pH and Ca at Tönnersa and at

Table 5. Soil nutrients (mmol/dm³) extractable in 0.5 M acetic acid. Average from 7 samples at various depths (cm) at Tönnersa (Tö) and Sandhammaren (Sh).

locality; plant community; depth	Na	K	Ca	Mg	Cl	S	P
Tö; Honkenyetum peplidis; 20-30	1.9±1.7	0.60±0.11	1.9±0.6	1.1±0.1	0.90±1.3	0.14±0.08	0.36±0.09
Tö; Salicetum arenariae Am. aren. subass.; 90-110	0.27±0.05	0.27±0.04	1.0±0.1	0.43±0.06	0.11±0.04	0.12±0.06	0.33±0.05
Tö; Salici-Empetretum Lophoc. heter. subass.; 0-10	0.55±0.09	0.93±0.15	2.0±0.4	0.96±0.18	0.26±0.06	0.28±0.18	0.29±0.15
Sh; Elymo-Ammophiletum typ. subass.; 20-30	0.31±0.08	0.41±0.23	3.3±0.4	0.52±0.10	0.15±0.07	0.20±0.06	2.0±0.3
Sh; Violo-Coryneporetum Cladonia subass.; 90-100	0.19±0.06	0.11±0.02	2.8±0.4	0.20±0.02	0.07±0.03	0.15±0.03	1.7±0.2
Sh; Salici-Empetretum Lophoc. heter. subass.; 0-10	0.22±0.07	0.54±0.18	1.2±0.2	0.43±0.06	0.27±0.05	0.22±0.09	0.43±0.14

Sandhammaren was not the same due to difference in substratum.

In 0.5 M HAc, the soluble amount of Na was low except just near the sea. In maritime sands Na is supplied mainly from salt spray. The leaching of Na is quite rapid. The standard deviation in the soil analyses is $\pm 3.2\%$ and in the plant analyses $\pm 1.3\%$.

The K concentration was low except in the organic layers inland from the seaward dunes. In coastal sands, the losses by leaching are compensated mainly by supply from the precipitation. The standard deviation in the soil analyses is $\pm 3.6\%$ and in the plant analyses $\pm 1.6\%$.

The Ca concentration in the soil was high. At Sandhammaren P seemed to be correlated with Ca. Ca mostly increased with organic matter. In the subsoil, however, Ca decreased with the age of the dunes (see Salisbury 1952 p. 300, Olson, J. 1958 p. 157), being leached. The standard deviation in the analyses is $\pm 4.3\%$ in the substratum and $\pm 1.5\%$ in the plant material.

The Mg concentration was low in the soil. The annual supply of Mg with the precipitation is in South Sweden 2–3 kg/ha (Eriksson, E. 1959 Fig. 2), but this figure is hardly valid for the maritime fringe. The standard deviation in the analyses is $\pm 4.6\%$ in the substratum and $\pm 0.7\%$ in the plant material.

Cl is very easily leached, the large supply being soon lost again. The standard deviation in the analyses is $\pm 5.0\%$ in the substratum and $\pm 1.5\%$ in the plant material.

The annual S supply from the precipitation is considerable, due both to spray of S-rich sea water, pollution and other sources. According to Ødelien (1967) there could be a S deficit in sandy soils along Norwegian coasts due to the strong leaching.

However, the present excess of sulphur compounds in the precipitation must provide enough S to the plants. The standard deviation in the analyses is $\pm 6.7\%$ in the substratum and $\pm 2.4\%$ in the plant material.

P could be quite strongly combined with Ca. The quotient between Ca and P at Sandhammaren is 1.5–1.7. Juo & Ellis (1968 pp. 375–380) have discussed the origin of Ca-P. From maritime sands in Great Britain Wright (1956 p. 35) has shown that both 'available' P and total P increase in the fine grain-sizes, which also seems to be the case in the northern part of Tönnersa. There are both mineral P and organic P in the soil. The main mineral part occurs as Ca-P except at too low pH. According to Williams & Saunders (1956 p. 104) the organic P in the sands probably occur to some extent in films coating the mineral particles. The standard deviation in the soil analyses is $\pm 3.9\%$ and in plant analyses $\pm 1.6\%$.

Horizontal distribution of the parameters in the surface soil

During the year the water content, as a whole, is lowest in the lichen-rich stands (5–60 g/dm³) and increases seawards and, in the humus layers, also landwards (Fig. 45). An exception is Cladonio-Coryneporetum in the inner dunes at Sandhammaren. In Elymo-Ammophiletum the amount of soil water was 25–70, in Salici-Empetretum 45–140, in Molinio-Myricetum gale Salix arenaria subass. 110–270 and in Caricetum acutae 340–540 g/dm³. In the oak and pine forests the water content was 110–270, in the birch fens ca. 500 and in the alder carrs ca. 700 g/dm³.

The organic matter increased inland from the beach (2–6 g/dm³) to the forest (30–80 g/dm³). In

Symbols a-e used in Figs. 45-55: (a) pure sand + drift vegetation + marram and sandy grassland vegetation; (b) dwarf-shrub and bush vegetation (*Salicetum arenariae* *Carex nigra* subass. and *Molinio-Myricetum gale* *Salix arenaria* subass. are included in the next category); (c) vegetation in wet and moist sites; (d) pine vegetation; (e) oak vegetation.

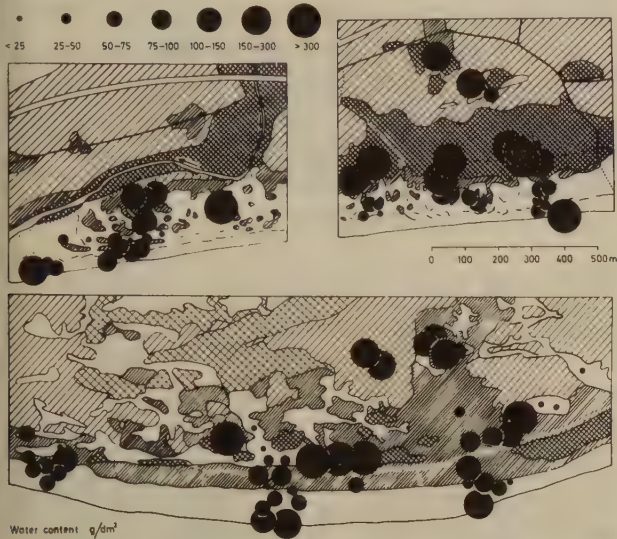


Fig. 45. Horizontal distribution of water content in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols, see above. In the seaward stands (from the shore line and ca. 150 m inland) mostly averages from 4-7 samples, in other stands from 1-3 samples.

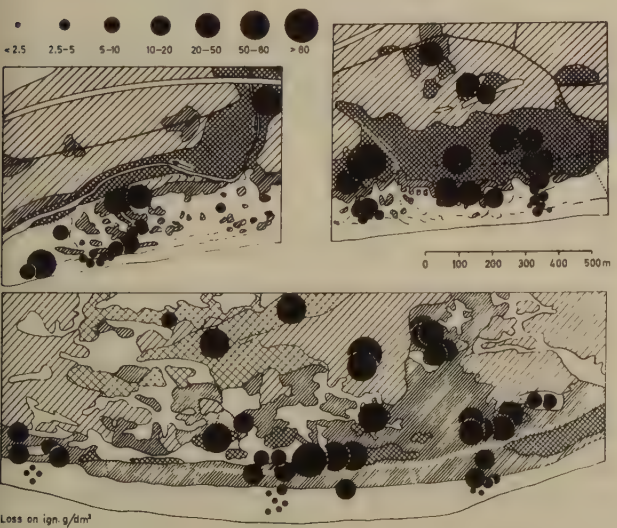


Fig. 46. Horizontal distribution of loss on ignition in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

Cakiletum maritimae the humus content was 6, in *Elymo-Ammophiletum* 2-9 and in *Violo-Corynephoretum* and *Cladonio-Corynephoretum* 3-13 g/dm³ (Fig. 46). Marshall (1967 p. 210) has reported a wide amplitude of the organic matter (0-7.6 %) below European *Corynephorus*-vegetation. In the present work the values do not exceed 1 %. In *Salici-Empetretum Festuca arenaria* subass. the amount of humus was 8 g/dm³. Some stands of *Salici-Empetretum Lophocolea heterophylla* subass. contained as much as 50 g/dm³, due to less exposure and high density of plant cover.

Wilson (1960) found an increase from 0.2 % in *Elymo-Ammophiletum* to ca. 13 % in the *Calluna* heath. The humus content is often higher in the pine forest than in the oak forest. In the raw humus of the *Deschampsia flexuosa* - *Pinus sylvestris* comm. the humus quantity was 130-140, in *Melampyro-Quercetum roboris Luzula campestris* var. about 110 and in *Calluna vulgaris* soc. ca. 60 g/dm³. In these three stands the organic matter was only 20, 4 and 13 g/dm³ respectively at a depth of 50-60 cm. *Vaccinio-Pinetum sylvestris Empetrum nigrum* subass. at Tönnersa was distinguished by a very sharp gradient in the surface soil from 75 at 0-5 cm to 10 g/dm³ at 5-10 cm. The dune depressions were in most cases characterized by a high humus content: *Salicetum arenariae Carex nigra* subass. with an average of ca. 20, *Molinio-Myricetum gale* ca. 40, *Caricetum acutae* 40-70, *Carex rostrata* - *Juncus*

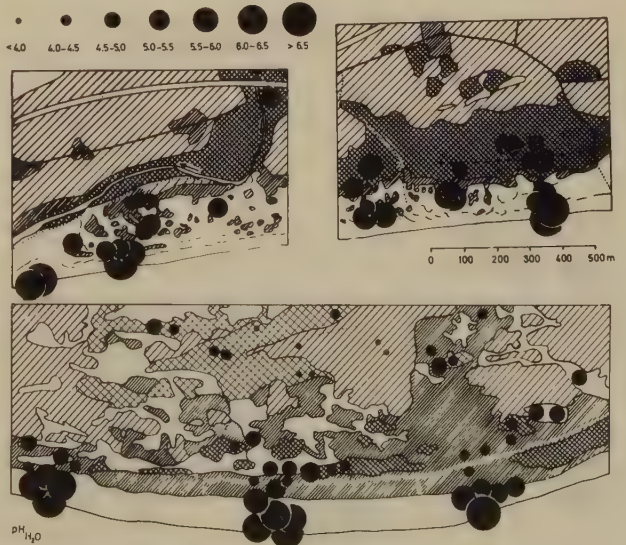


Fig. 47. Horizontal distribution of pH(H₂O) in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

effusus comm. often exceeding 80, birch fens 40–80, alder carrs 110 g/dm³. Ranwell (1959) has studied the humus accumulation in English dune slacks and found that the amount of humus is reduced in the wettest sites.

The soil reaction varied between pH 4–7 (in KCl 3–6) in dry habitats and 4.5–5.5 (3.5–4.5) in moist or wet habitats. Ranwell (op.cit.) has reported a pH amplitude of 4.4–8.5 (4.1–7.8). In calcareous dunes the amplitude is narrower, pH 8–9 (see Willis et al. 1959). The highest pH was found on the naked beach with an average of 6.9 (6.2). Inland from the beach there was an obvious decrease (Figs. 47–48): Elymo-Ammophiletum with an average of ca. 6 (in KCl 5), Violo-Corynephorretum and Cladonio-Corynephorretum 4.5–5.0 (3.5–4.0), Salici-Empetretum 4.0–5.0 (3.0–4.0). Gorham (1958 p. 375) has reported a decrease from 8.2 to 5.7, Wilson (op.cit.) from 7.0 to about 4.0. The lowest pH was registered from *Deschampsia flexuosa* - *Pinus sylvestris* comm. at Sandhammaren, pH < 4.0 (in KCl < 3.0). *Caricetum acutae*, *Irido-Alnetum glutinosae* and *Filipendulo-Alnetum glutinosae* were distinguished by somewhat higher pH values than those of *Molinio-Myricetum gale Salix arenaria* sub-ass., *Caricetum canescentis-nigrae* and *Polytrichobetuletum pubescentis*. In the latter group pH was in general below 5.0 (< 4.0). As seen from Figs. 47–48, pH as a whole was lower at Sandhammaren than at Tönnersa, especially in the dune depressions.

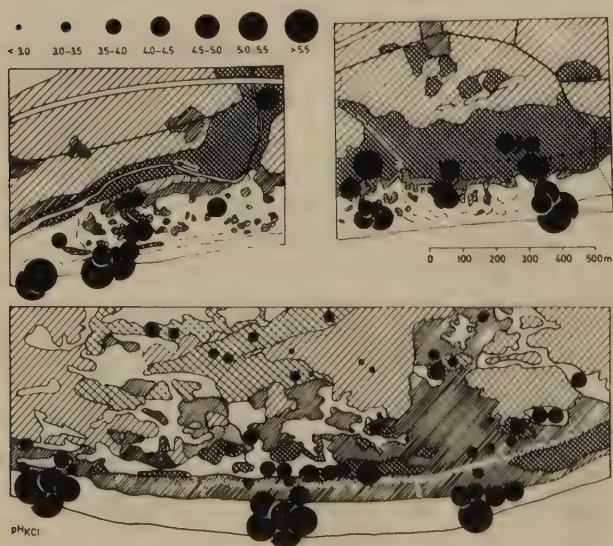


Fig. 48. Horizontal distribution of pH(KCl) in the surface soil. Samples from 1966–1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

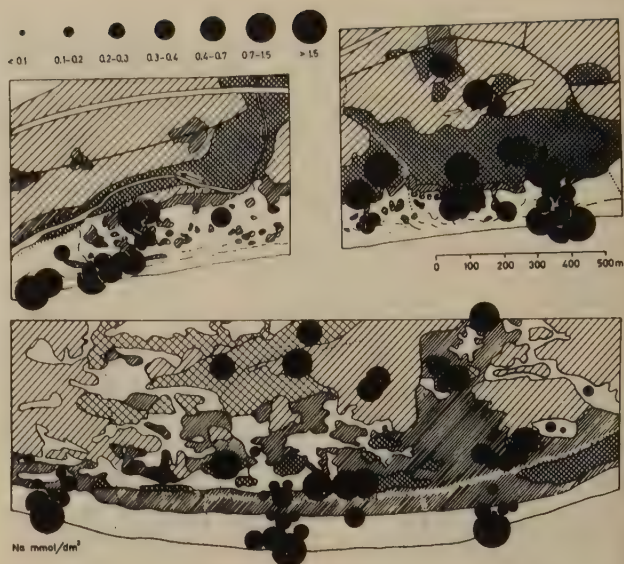


Fig. 49. Horizontal distribution of Na in the surface soil. Samples from 1966–1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

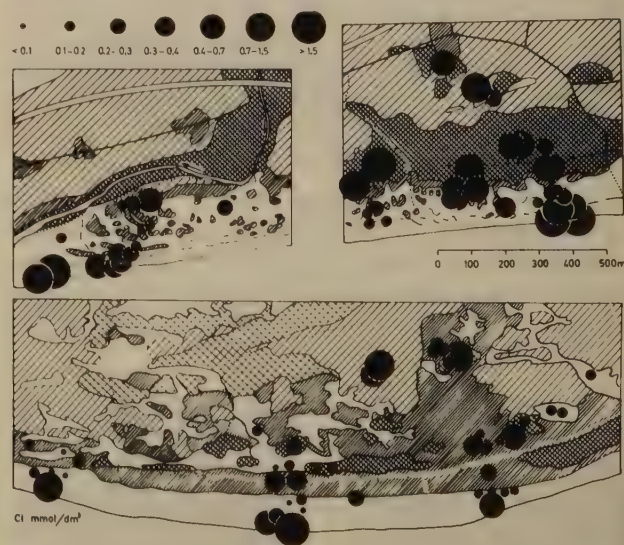


Fig. 50. Horizontal distribution of Cl in the surface soil. Samples from 1966–1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

The concentrations of Na and Cl (Figs. 49–50) were higher at Tönnersa than at Sandhammaren. On the naked beach high values were registered. Sometimes there may be higher values on the naked beach at Sandhammaren, when the pores in the soil are filled with sea water. As seen in Figs. 49 and 50 the salinity decreased landward more rapidly at Sandhammaren. The concentrations of both Na and Cl were there low in the pure sand of Elymo-Ammophiletum. Very low Na and Cl values (< 0.2 mmol/dm³) were measured in Violo-

Corynephorum and Cladonio-Corynephorum. In the very dry sand the content of Cl ($< 0.1 \text{ mmol/dm}^3$) seemed to be less than that of Na. Both elements increased in Salici-Empetretum and continued to increase further landwards in various forest habitats ($0.5\text{--}1.0 \text{ mmol/dm}^3$) rich in litter and humus. These latter figures exceeded those of exchangeable Na in inland Swedish natural moor soils (Sjörs 1961 Table 1). In the dune depressions at Tönnersa Na and Cl had rather high concentrations ($> 1.0 \text{ mmol/dm}^3$); especially Cl had much higher compared with corresponding samples from the dune depressions at Sandhammaren. Na and Cl (besides K) had been enriched in Irido-Alnetum glutinosae. Normally Na exceeded K, which is also reported from English dune slacks (see Willis et al. 1959 p. 16, Crawford & Wishart 1966 p. 737).

K is the third analysed monovalent ion but with somewhat different features compared with Na and Cl. The K concentration was a little higher at Tönnersa than at Sandhammaren. On the beach the concentration of K was moderately high, and much lower than those of Na and Cl. A special increase was found in Honkenyetum peplidis and Cakiletum maritimae (Fig. 51). In Elymo-Ammophiletum the values for K and also for S were in many cases the lowest for all determined elements, which is probably a result of the nutrient uptake by the vegetation. K decreased inland from the beach to Elymo-Ammophiletum Hieracium umbellatum ssp. subass.

Small amounts of K ($< 0.2 \text{ mmol/dm}^3$) were also found in lichen-rich vegetation (Fig. 51). Further inland there was an increase of K in the humus layers. At Tönnersa the K quantities in forests and dwarf shrub heaths may be of the same magnitude as in the dune depressions, $0.7\text{--}1.5 \text{ mmol/dm}^3$, or in Irido-Alnetum glutinosae even higher. Much smaller amounts were recorded from the birch fens ($0.2\text{--}0.4 \text{ mmol/dm}^3$) and various stands with sedges at Sandhammaren.

Ca is the predominant cation. Of the bivalent ions Ca was highest in the dry habitats at Sandhammaren and the wet environments at Tönnersa (Fig. 52). Both Mg and S showed higher values from Tönnersa as a whole. Ca and Mg had high figures in Salicetum arenariae and Molinio-Myricetum gale Salix arenaria subass. as a consequence of the mineral supply from the litter fall. High quantities were recorded from Cakiletum maritimae and Honkenyetum peplidis (Fig. 52, 53), an average of ca. 2 for Ca and ca. 1 mmol/dm^3 for Mg. In the seaward stands of Sandhammaren the amounts of $\text{Ca} > 2.5 \text{ mmol/dm}^3$ were due to the substratum being rich in a Ca-P compound. Mg was much lower, often $< 0.4 \text{ mmol/dm}^3$ (Fig. 53). Here the decrease inland in concentration of Ca and also P was obvious and there were extremely low values in Cladonio-Corynephorum, $\text{Ca} < 0.5$ and $\text{Mg} < 0.25$.

Gorham (1958) reported only small amounts of Ca from stable dunes. On sites where ligneous plants

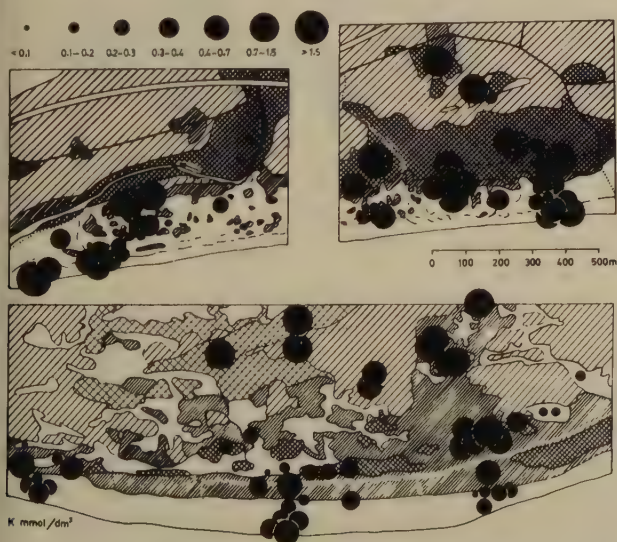


Fig. 51. Horizontal distribution of K in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

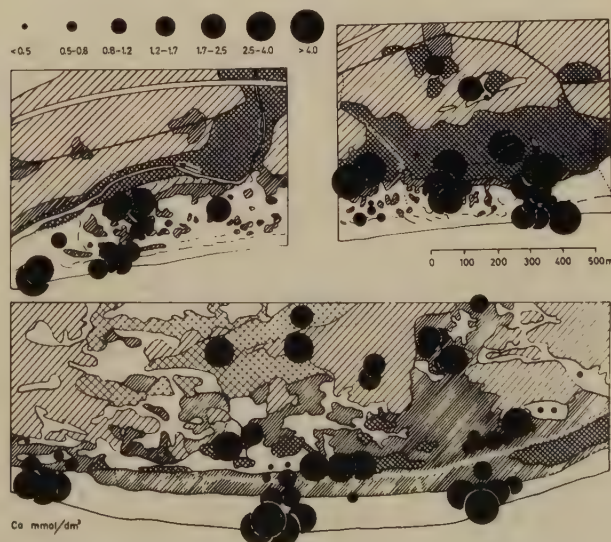


Fig. 52. Horizontal distribution of Ca in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

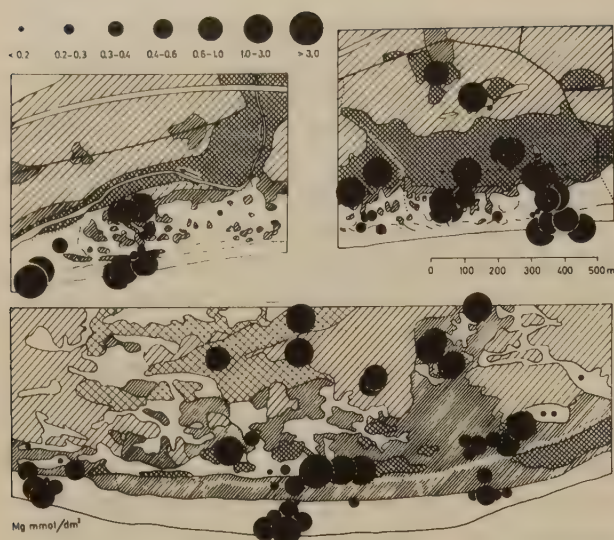


Fig. 53. Horizontal distribution of Mg in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

are prevalent the metal sequence is $\text{Ca} > \text{K} > \text{Mg} > \text{Na}$. In the dune depressions it is $\text{Ca} > \text{Mg} > \text{Na} > \text{K}$. The phenomenon that Ca was accumulated in *Caricetum acutae* and *Irido-Alnetum glutinosae* ($> 4 \text{ mmol/dm}^3$) is possibly an effect of inundation. The concentrations of Ca and Mg were equally high in the alder carrs on the west coast and in *Carex rostrata* — *Juncus effusus* comm. at Sandhammaren. The concentration of Ca, and often K, increased much more in the forests than did that of Mg (the latter more similar to Na and Cl). In the O-layers of *Calluna vulgaris* soc. and *Deschampsia flexuosa* - *Pinus sylvestris* comm. K and Ca contents were similar. In the oak forest the amount of Ca was higher, also in the subsoil, where in the pine forest Fe had replaced Ca.

S and P had similar values in the lichen-rich stands. In general the S-concentration was very low (Fig. 54). In the dune depressions there was more 'available' S than P, both possibly also in storage. There were high quantities of S in *Caricetum acutae* and *Irido-Alnetum glutinosae*, $\text{S} > 0.4 \text{ mmol/dm}^3$, compared with $\text{S} < 0.2$ in the pure sand. The 'available' P had much higher values in the mineral soil than in the organic layers (Fig. 55). Wright (1956) has estimated that total P is about 20 times as high as 'available' P in a British dune area. In the seaward dunes at Sandhammaren the quantities of P ($> 2 \text{ mmol/dm}^3$) as well as of Ca were considerable and much higher than those at Tönnersa. There were

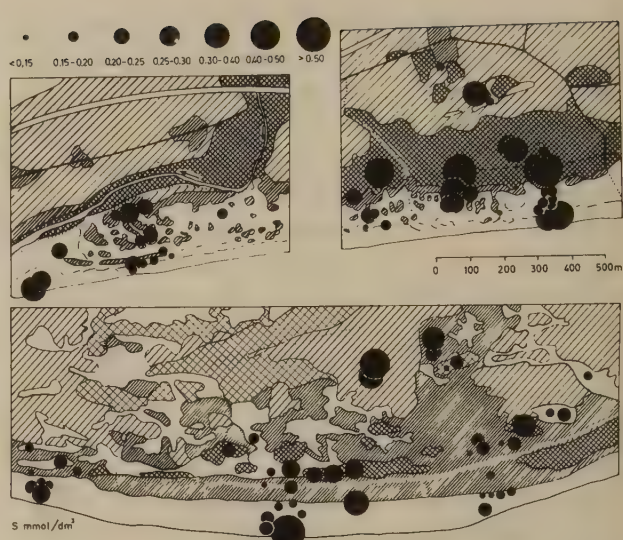


Fig. 54. Horizontal distribution of S in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

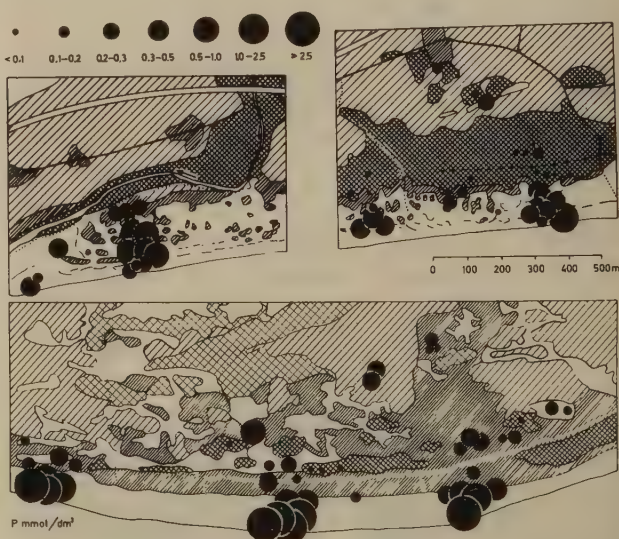


Fig. 55. Horizontal distribution of P in the surface soil. Samples from 1966-1971. Above: Tönnersa; below: Sandhammaren. — Symbols and explanation, see Fig. 45.

only small amounts of P in *Cladonio-Corynephorum* ($< 0.3 \text{ mmol/dm}^3$). In the hydromorphous soils the P-concentration was reduced and often much lower than 0.1 mmol/dm^3 . A greater part of the total P could possibly be stored in the humus. Holmen (1964 p. 166) says that the storage of P in peat is lower than that in mineral soil. In the acid humus at Sandhammaren P had higher values than at Tönnersa and was similar to P concentrations in mires (see Malmer 1962 p. 198).

Vertical distribution of the parameters in the subsoil

At Tönnersa the water content increased with depth on the naked beach (1), in Elymo-Ammophiletum *Hieracium umbellatum* ssp. subass. (4) and *Salicetum arenariae* *Carex nigra* subass. (7). A downward decrease of the soil water, on the other hand, was found in Elymo-Ammophiletum typical subassociation (3) and *Salici-Empetretum* *Lophocolea heterophylla* subass. (9). In other investigated stands, such as Honkenyetum *peplidis* (2), *Salicetum arenariae* *Ammophila arenaria* subass. (6) and *Salici-Empetretum* *Festuca arenaria* subass., the differences in the soil profile were small (Fig. 56). At Sandhammaren the water content increased with depth in the naked beach (1), in Elymo-Ammophiletum *Salsola kali* var. (2), Elymo-Ammophiletum typical subass. (3) and *Cladonio-Corynephorretum* (stands 7 and 8). A downward decrease of the soil moisture was observed in Elymo-Ammophiletum typical subass. (4) and *Salici-Empetretum* *Lophocolea heterophylla* subass. (9). There were only small changes in Elymo-Ammophiletum *Hieracium umbellatum* ssp. subass. (5) and *Violo-Corynephorretum* *Cladonia* subass. (6) (Fig. 57).

In the beach at Tönnersa the soil water content was low throughout from May to August (70 g/dm^3) but rose during the winter (seasonal variation was

measured only in 1966–1967). The rise was more pronounced at Sandhammaren. In stand 2 at Tönnersa there were low values in the surface soil during all the year. At Sandhammaren peaks occurred in stand 2 in March and July. In December the surface soil was wetter than the subsoil. In stand 3 at Tönnersa the soil moisture had low values throughout the soil profile but with maxima in August and December (ca. 50 g/dm^3). Higher values were recorded from stand 3 at Sandhammaren, as a result of slower percolation. In stand 4 at Sandhammaren a minimum was found in September. In stand 4 at Tönnersa only 5 g/dm^3 was measured in August, which is remarkable as the precipitation may have been high. At the level of 90–100 cm there was a high soil moisture in March and May. In stand 5 at Sandhammaren small water amounts were measured in September. In stand 5 at Tönnersa the water content was about 50 in the summer and 100 g/dm^3 in the winter. Low summer values are partly an effect of strong evaporation and possibly also (see Willis & Jefferies 1963, Rychnovská & Kvet 1963) due to increased transpiration of various dune plants. In stands 6–8 at Sandhammaren the surface soil was much drier than the subsoil possibly due to difficult infiltration of precipitation water. The dry surface layer protects the subsoil from drying out. In stand 7 at Sandhammaren the water content was

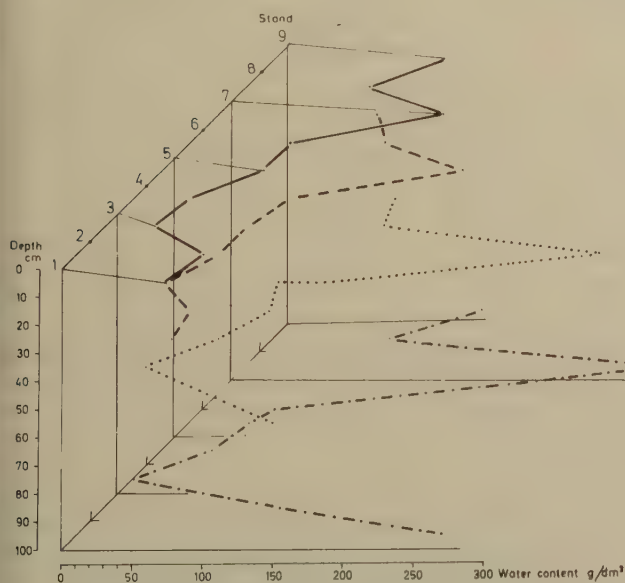


Fig. 56. Tönnersa. Vertical distribution of water content in the subsoil. Average from 7 sample series 1966–1967. — For stands 1–9, see Fig. 43.

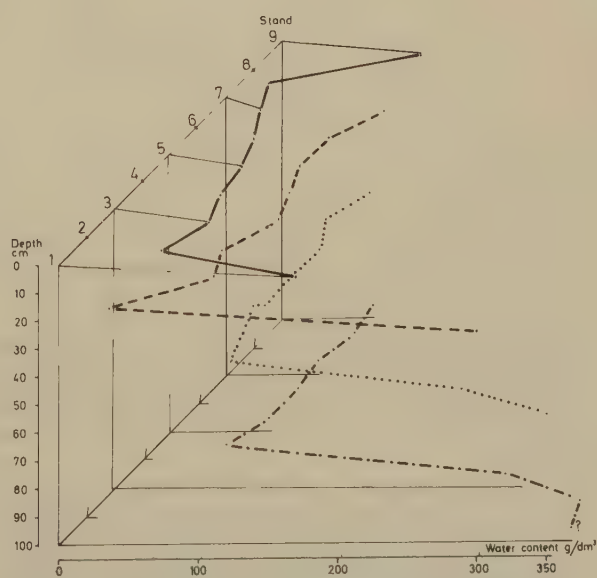


Fig. 57. Sandhammaren. Vertical distribution of water content in the subsoil. Average from 7 sample series 1966–1967. — For stands 1–9, see Fig. 44.

only 2 g/dm³ in the surface soil in August. In stand 6 at Tönnersa maxima were recorded in March and December. In the latter month there was also a peak in stand 8 at Tönnersa. The values were 75–100 g/dm³. In stand 7 at Tönnersa the variation in water content between the seasons was due to inundation. As a consequence of the higher amount of humus also the water content was higher in stands 9 at Tönnersa and 9 at Sandhammaren. At the first locality there were peaks at 90–100 cm in March and September. At the second locality small values were reported in late summer.

The organic matter was somewhat less at Sandhammaren than at Tönnersa. A landward gradient in the stands 1–4 was not so obvious. In the stands 5–9 at Tönnersa the amount of humus increased and reached 32 g/dm³ as maximal value. Downward in the soil profiles the organic matter rapidly decreased (Fig. 58). In the stands 1–4 at Sandhammaren, however, the organic matter underwent no obvious downward changes in the soil profiles. A downward decrease was observed in the stands 5–9 there, especially evident in the upper layers. Maximal value was 22 g/dm³ (Fig. 59). A seasonal variation was difficult to notice, only slightly in evidence on the beach. In stands 3–4 at

Tönnersa and 3–5 at Sandhammaren there was an irregular annual variation, in March possibly an increase in the surface soil. In stand 6 at Tönnersa there was a minimum in summer and a maximum in winter and spring, due to the litter fall. The irregularities of the soil profile in stand 8 at Tönnersa were due to presence of humus lenses. In the stands 9 at Tönnersa and 9 at Sandhammaren the organic content was much higher in the surface soil than in the subsoil.

The pH increased with depth in the stands 4–5 and 8–9 at Tönnersa. In stand 5 the increase was 2.5 units (Figs. 60, 62). The course of the curves in the stands 2–3 and 6–7 were more vertical. In the stands 1–4 at Sandhammaren pH was rather similar in the soil profiles. In the stands 5–9 a downward increase occurred (Figs. 61, 63). In stand 9 at Sandhammaren the amplitude was about 1.3 pH-units. As a whole the pH interval in the soil from the surface to a depth of one metre was much narrower at Sandhammaren than at Tönnersa, but most evident in the lichen-rich sites. Wilson (1960 p. 355) has shown a vertical difference of 1.0–1.3 pH-units.

On the naked beach pH was lowest in May and highest in September due to sea water influence. In the stands 2–3 at Tönnersa and 3–4 at Sandham-

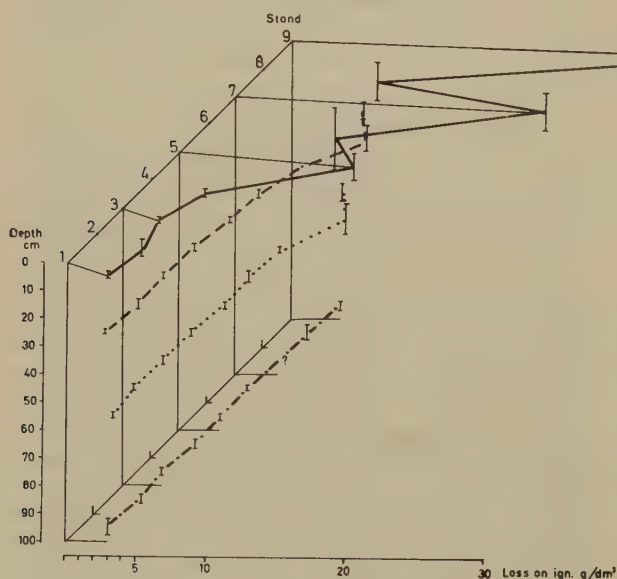


Fig. 58. Tönnersa. Vertical distribution of loss on ignition in the subsoil. Average from 7 sample series 1966–1967. — For stands 1–9, see Fig. 43. — The standard deviation is illustrated as vertical lines. The value of the amplitude, see the horizontal scale below.

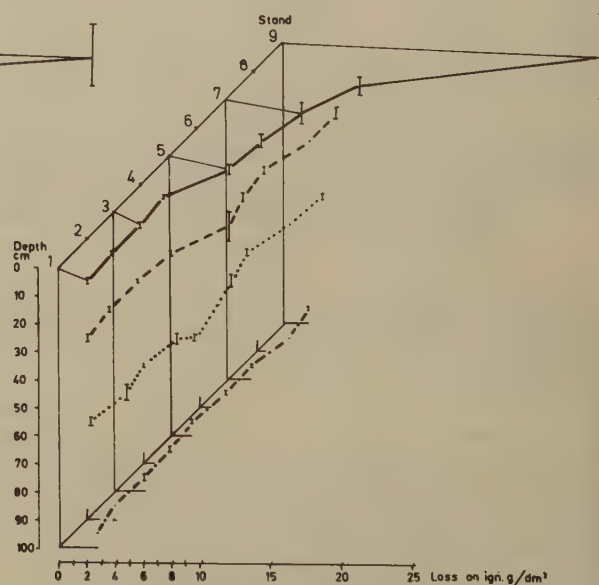


Fig. 59. Sandhammaren. Vertical distribution of loss on ignition in the subsoil. Average from 7 sample series 1966–1967. — For stands 1–9, see Fig. 44. — Standard deviation illustrated as in Fig. 58.

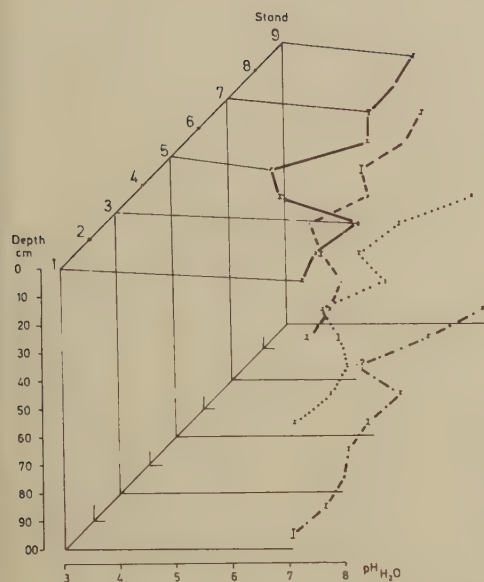


Fig. 60. Tönnersa. Vertical distribution of $\text{pH}(\text{H}_2\text{O})$ in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

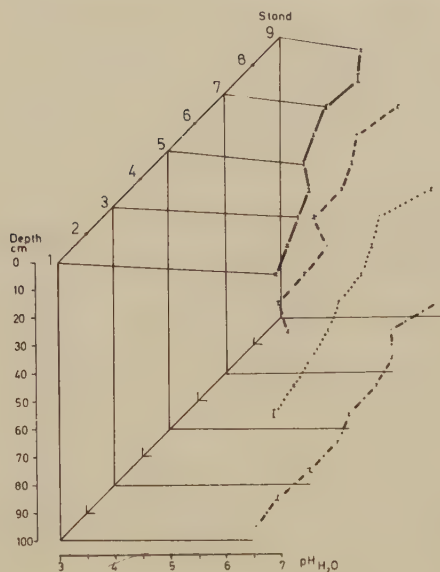


Fig. 61. Sandhammaren. Vertical distribution of $\text{pH}(\text{H}_2\text{O})$ in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44. For further explanation, see Fig. 58.

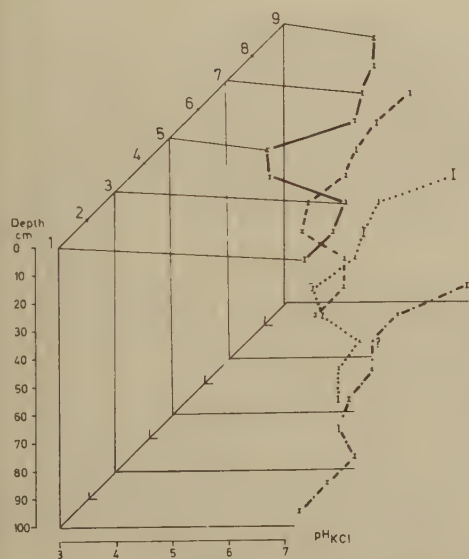


Fig. 62. Tönnersa. Vertical distribution of $\text{pH}(\text{KCl})$ in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

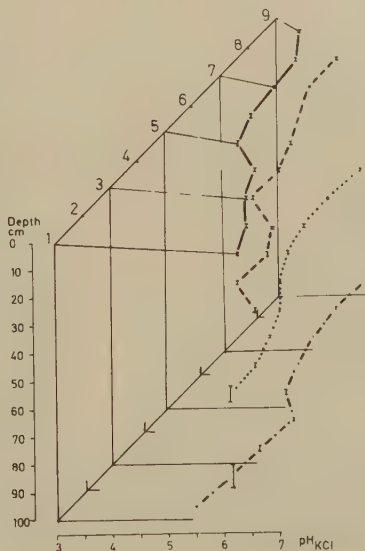


Fig. 63. Sandhammaren. Vertical distribution of $\text{pH}(\text{KCl})$ in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

maren there was a pH-minimum in August and a maximum in the autumn. The trend was less distinct at Sandhammaren. In the stand 4 at Tönnersa and stand 5 at Sandhammaren the lowest pH values were measured in late summer. In the lichen-rich stands 5 at Tönnersa and 6-8 at Sandhammaren there were

no obvious changes during the year. In stand 6 at Tönnersa pH decreased in May and September. The latter month seemed to show a minimum in the stands 9 at Tönnersa and 9 at Sandhammaren.

The courses of Na and Cl in the vertical distribution were similar (Figs. 64-67) and the curves il-

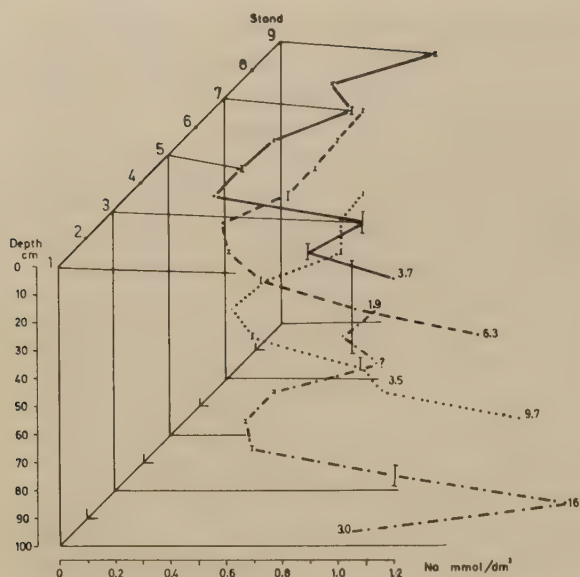


Fig. 64. Tönnersa. Vertical distribution of Na in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

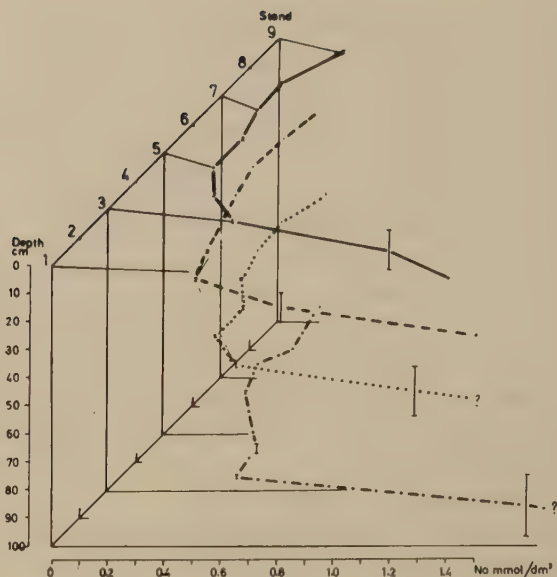


Fig. 65. Sandhammaren. Vertical distribution of Na in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

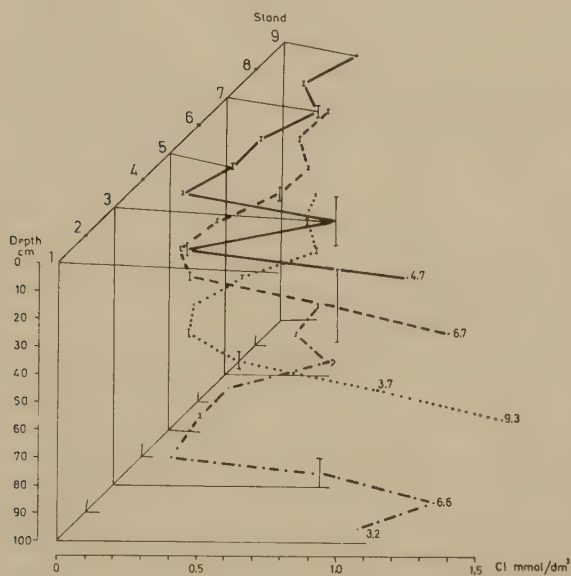


Fig. 66. Tönnersa. Vertical distribution of Cl in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

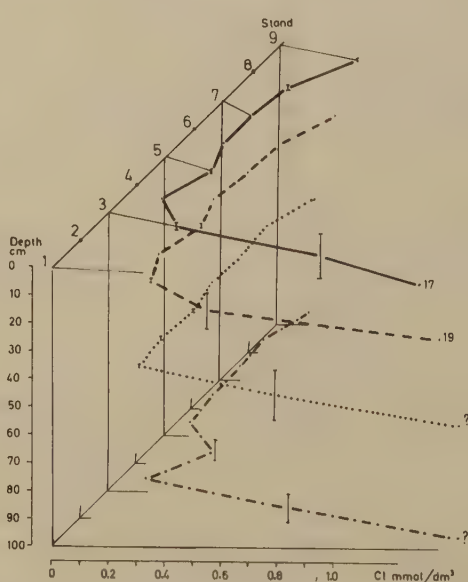


Fig. 67. Sandhammaren. Vertical distribution of Cl in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

illustrate distinctly the sharp salinity gradient, less regular at Tönnersa than at Sandhammaren. In the stands 1-2 at Sandhammaren the concentrations of Na and Cl were high in the whole soil profile. Landwards the values decreased strongly, especially in the lichen-rich stands. In stand 7 an average of Na at 90-100 cm was 0.15 mmol/dm^3 and of Cl only

0.07. A small increase for both elements was registered in stand 9. At Tönnersa there were higher values of both Na and Cl in the surface soil of stand 3 compared with that of stand 2. In the subsoil the condition was the reverse. Landwards in the stands 4-9 the values were much lower. Small rises were found in the stands 7 and 9. An average in stand 5 at

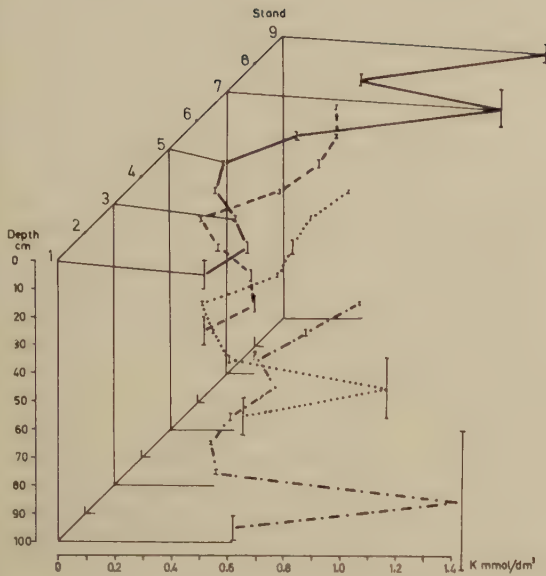


Fig. 68. Tönnersa. Vertical distribution of K in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

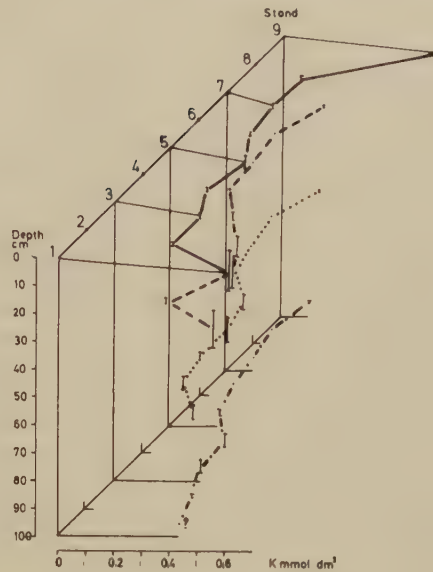


Fig. 69. Sandhammaren. Vertical distribution of K in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

90–100 cm showed 0.27 mmol/dm^3 Na and 0.11 Cl . In the stands 1–4 and 6 at Tönnersa Na and Cl had their highest concentrations in September and March. In the stands 8–9 at Tönnersa Na and Cl had low values in the summer. At Sandhammaren there were a maximum in winter and minimum in summer.

K underwent very small changes or decreased with the depth in most stands (see Wright 1956 p. 36). An increase was found in Honkenyetum peploidis. In the surface soil K was rather similar at Tönnersa and Sandhammaren (Figs. 68–69), in the subsoil much higher at Tönnersa especially in the seaward stands. In stand 2 there at 50–60 cm the K concentration was about 1.1 mmol/dm^3 compared with only 0.4 in stand 2 at Sandhammaren. On the beach at Tönnersa K had a peak in September, at Sandhammaren during the whole autumn. In stand 9 at Sandhammaren the lowest K value in the surface soil was recorded in March.

At Tönnersa the vertical distribution of Ca resembled that of Mg (Figs. 70–73), which was different from Sandhammaren where Mg showed a trend more similar to Na and Cl. The Ca changes in the soil profile were smaller at Tönnersa than those at Sandhammaren, where an increase with depth occurred in most stands (Fig. 71). Both Ca and Mg showed high values in the stands 6–7 at Tönnersa;

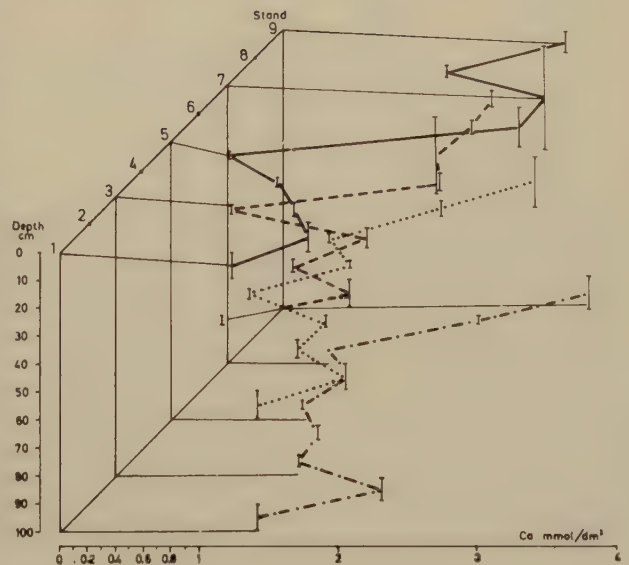


Fig. 70. Tönnersa. Vertical distribution of Ca in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

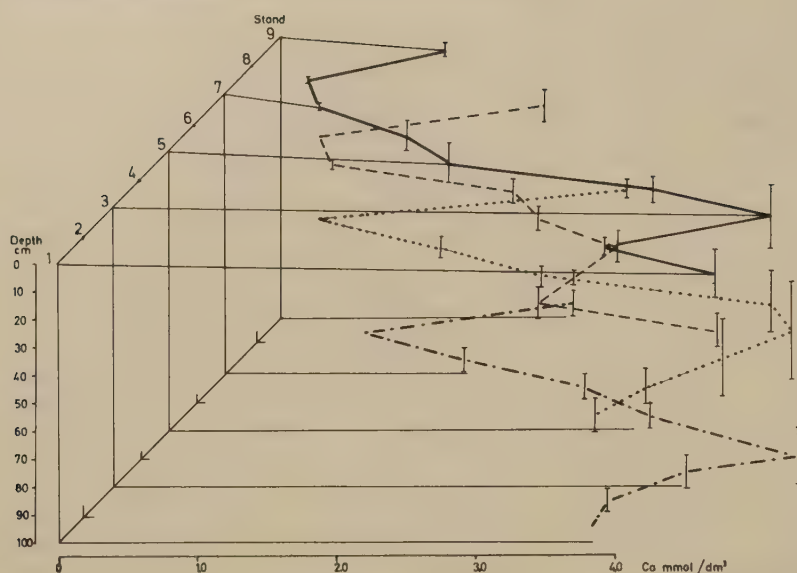


Fig. 71. Sandhammaren. Vertical distribution of Ca in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

at 0–10 cm Ca was about 2 and Mg ca. 0.8 and at 50–60 cm Ca about 0.5 and Mg ca. 0.3 mmol/dm³. The concentration of Ca at Sandhammaren was dependent on the substratum. In Fig. 71 the curves from different layers showed their highest Ca values in the stands 2–4. In stand 3 the Ca concentration was about 4.5 mmol/dm³ compared with 0.7 for Mg. Both values were much lower in stand 8 at the same level, Ca 0.40 and Mg 0.11 mmol/dm³. A seasonal variation in Ca had not been observed except in

stand 5 at Tönnersa, where a decrease in late autumn was replaced by an increase until March. A corresponding course was also observed for Mg, which in the stands at Tönnersa showed some peaks in September and March.

The courses of the curves for P were very different when comparing Tönnersa and Sandhammaren. At the first locality a small landward increase was found at all levels (Fig. 74). At Sandhammaren the P and the Ca curves had similar trends (Fig. 75), though

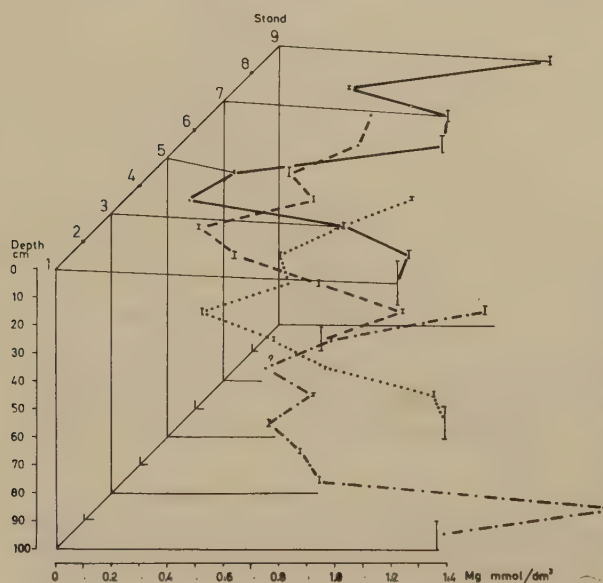


Fig. 72. Tönnersa. Vertical distribution of Mg in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

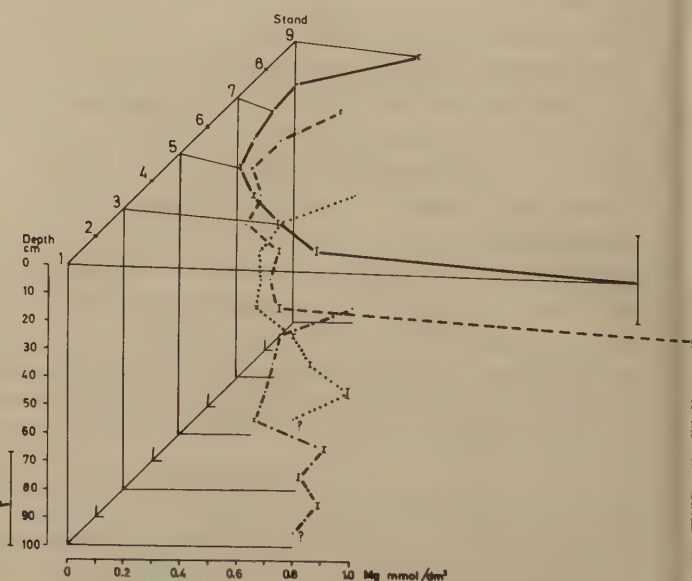


Fig. 73. Sandhammaren. Vertical distribution of Mg in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

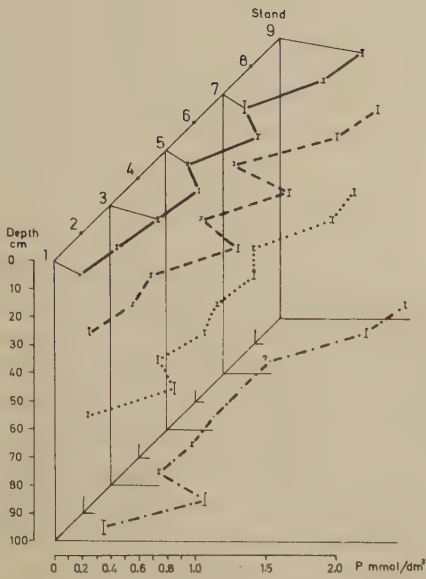


Fig. 74. Tönnersa. Vertical distribution of P in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

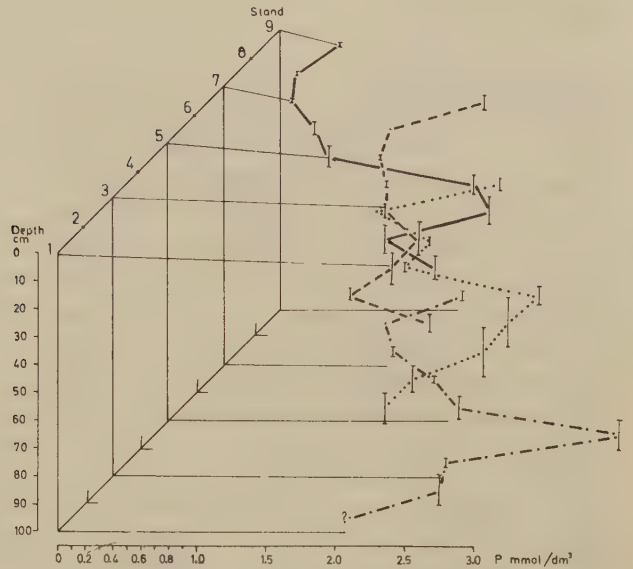


Fig. 75. Sandhammaren. Vertical distribution of P in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

the P concentrations were lower; however, in the mineral soil they were in most stands much higher than those of Tönnersa. At 20–30 cm in the stands 9 at Tönnersa and 9 at Sandhammaren about 0.7 and 1.5 mmol/dm³ respectively were measured. In stand 5 at Tönnersa P was low in late summer and high in

The diagrams for the S concentration (Figs. 76–77) were similar in the two localities. The gradient was not pronounced. On many occasions the values were the same, 0.1–0.2 mmol/dm³. In the stands 1–2 at Tönnersa higher S concentrations were recorded in September and March.

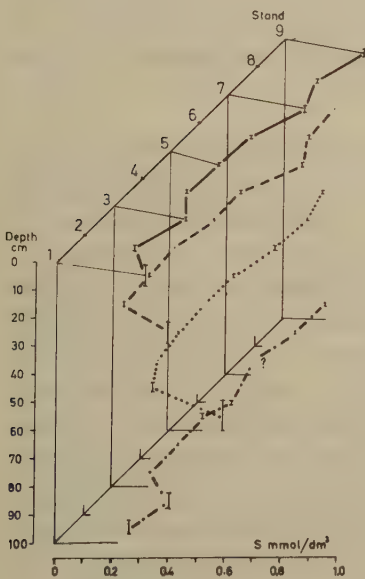


Fig. 76. Tönnersa. Vertical distribution of S in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 43; for further explanation, see Fig. 58.

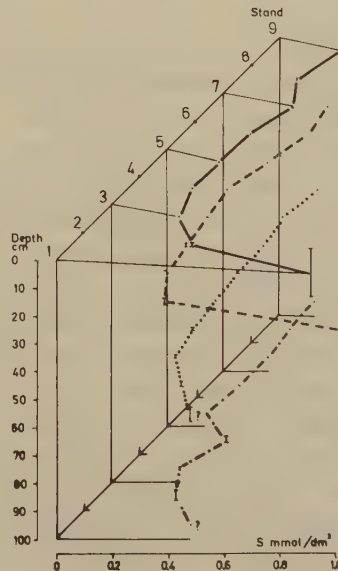


Fig. 77. Sandhammaren. Vertical distribution of S in the subsoil. Average from 7 sample series 1966-1967. — For stands 1-9, see Fig. 44; for further explanation, see Fig. 58.

Plant cover

Parts of an ecosystem

The plant cover has been divided into dead material and above ground phytomass or standing crop including the fractions: (a) dwarf shrubs, (b) herbs, graminids and ferns, (c) bryophytes and lichens. These fractions consist of assimilating and non-assimilating parts.

The mineral elements are divided into plant-bound nutrients in both plant cover and soil, available nutrients in the soil and storage nutrients (see below). The proportions in the phytomass and litter are illustrated in Figs. 78–90.

	Standing crop	Dead material	Mineral elements
Plant cover	dwarf shrubs	litter	plant-bound nutrients
	herbs, graminids, ferns		
	lichens, bryophytes		
Soil	roots, rhizomes	root litter	plant-bound nutrients
		humus	available nutrients
			storage nutrients

Dry weight and water content of standing crop and litter

The dry weight in *Honkenyetum peploidis* (Fig. 78) at Tönnersa and *Elymo-Ammophiletum Salsola kali* var. (Fig. 79) at Sandhammaren was only a small part of the fresh weight with a water content of 80 %. As seen in Figs. 80–81 the maximal dry weight in *Elymo-Ammophiletum* typical subassociation occurred in July–August, in most stands 400–800 g/m². The water content was 60–70 %; in the summer higher in the living shoots but otherwise higher in the litter. In *Elymo-Ammophiletum Hieracium umbellatum* ssp. subass. (Figs. 82–83) the litter constituted the main part of the dry weight. Smaller dry weights were measured at Sandhammaren than at Tönnersa. Three fractions were distinguished in *Violo-Corynephorum Cladonia* subass. (Figs. 84–85) and *Cladonio-Corynephorum* (Figs. 86–88). The dry weight was here no less than 80–90 % of the fresh weight. In most stands the dry weight varied between 100 and 400 g/dm²; in some blow-outs it was below 100 g/m² (Fig. 86).

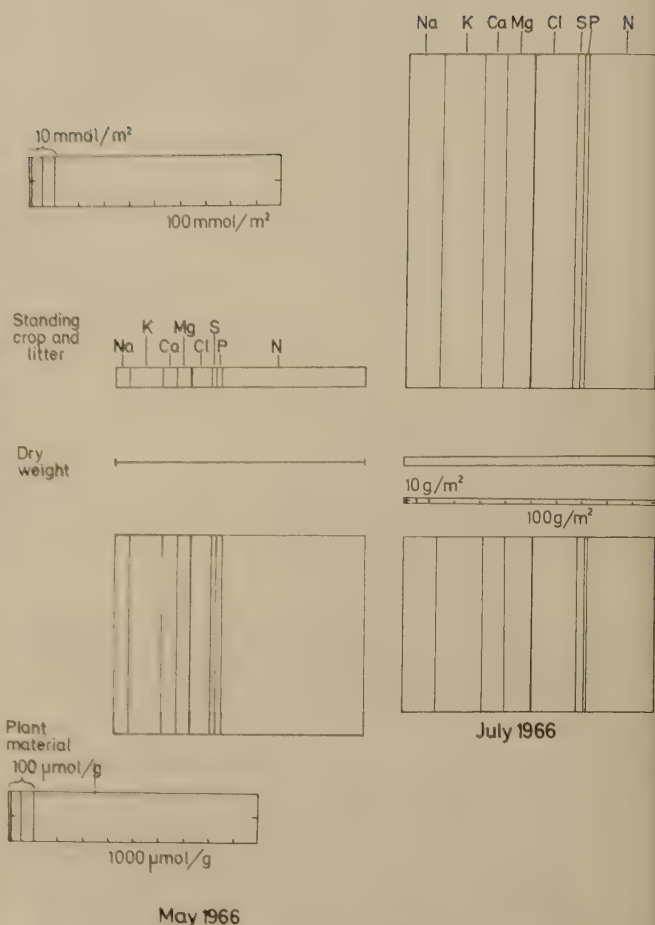


Fig. 78. Tönnersa. *Honkenyetum peploidis*. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 2, see Fig. 43; for symbols, see Fig. 79. The scales are area scales with a common base line. The height is a multiple of 2.

The dry weight in *Salicetum arenariae Ammophila arenaria* subass. was highest in the summer (Fig. 88) when 700 g/m² was measured. The water content, increasing in the autumn, was about 50 %. In *Salici-Empetretum* the water content was strongly variable. In *Festuca arenaria* subass. the dry weight seemed to be highest in the summer, ca. 350 g/m² (Fig. 89). In *Lophocolea heterophylla* subass. the dry weight in most stands was as high as 800–1000 g/m². The dwarf shrub fraction was most important followed by the litter or by bryophytes and lichens. Mork (1946 p. 345) has in forests reported a standing crop of *Calluna vulgaris* up to 1400 and *Empetrum hermaphroditum* up to 900 g/m². Of the total biomass about one half was below ground. The annual litter fall of the two nano-chamaephytes had been estimated to 260 and 210 g/m² respectively. Cormack

& Gimingham (1964) have indicated a litter production of *Calluna vulgaris* of 6 g/year in the pioneer stages and 70 g/year in the degenerated stages. Chapman, S.B. (1967) has estimated the increase in standing crop to 2400 g/m² and in accumulated litter to 1700 g/m² after 35 years.

Mineral nutrients in the plant material

In Honkenyetum peplidis the sum of the metals was one half of the total content of nutrients. In the summer the following metal sequence was found: $K > Na > Mg > Ca$. The high K concentration was similar to that of Cl (620–630 $\mu\text{mol/g}$). In Elymo-Ammophiletum *Salsola kali* var. at Sandhammaren (Fig. 79) the metal range was: $K \gg Mg = Ca > Na$. Only K is of the same concentration as in the previous stand. The Na concentration was much lower (ca. 20 $\mu\text{mol/g}$), which is a typical feature in the above ground phytomasses at Sandhammaren. Possibly Ca has to be liberated in the soil to compensate for the Na uptake in the presence of Cl (see Elgabaly 1962 pp. 157–164). The N content was higher than those of S and P. The composition of mineral elements in putrified tang was different

(Table 7) from that in the above mentioned stands. Of interest are the proportions between S (ca. 1000 $\mu\text{mol/g}$) and P (60–80 $\mu\text{mol/g}$). Thus only very small amounts of P from cast up seaweeds were supplied to the landward ecosystems.

In Elymo-Ammophiletum typical subass. at Tönnersa the metals were a third of all measured nutrients. The metal sequence resembled that of Honkenyetum peplidis. The non-metal sequence was: $N > Cl \gg S = P$ (Fig. 80). At Sandhammaren the metals were also a third of the mineral elements, in the litter only a fourth. The metal sequence was: $K \gg Ca = Mg > Na$. In the litter Ca was always higher than Mg. According to Thenabadu (1968 pp. 132–143) Mg and Na have the ability to counteract the uptake of K and Ca by the vegetation through cation antagonism. At both Tönnersa and Sandhammaren there was a gradual decrease of the sum of nutrients in the plant material from May 1966 to March 1967. In the latter month only one fraction has been distinguished. In Elymo-Ammophiletum *Hieracium umbellatum* spp. subass. the metals were about a fourth of all measured nutrients. In the summer the metal sequence was

Table 6. Nutrients ($\mu\text{mol/g}$) in plant material at Tönnersa (Tö) and Sandhammaren (Sh).

locality; season; plant community; type of sample	Na	K	Ca	Mg	metals, total	Cl	S	P	N	elements, total
Tö; March 1967; seaweeds cast up on the beach	670	640	460	520	2300	620	1400	60	2500	6900
Sh; March 1967; seaweeds cast up on the beach	890	670	420	450	2400	1000	600	80	1800	5900
Tö; May 1966; Salicetum arenariae Am.aren.subass.;										
Salix arenaria leaves	16	190	190	80	480	19	58	110	2100	2800
Tö; July 1966; do.; do.	23	210	180	78	490	55	47	49	1300	1900
Tö; July 1966; do.; do., renewed cutting	8	400	130	120	660	30	68	83	2000	2800
Tö; May 1966; Salici-Empetretum Fest.aren.subass.;										
Empetrum leaves	12	140	150	64	370	34	37	25	530	990
Tö; July 1966; do.; do.	14	170	110	68	360	40	37	38	500	980
Tö; Dec. 1966; do.; do.	11	120	130	67	330	21	38	39	450	880
Tö; May 1966; Salici-Empetretum Lophoc.heter.subass.;										
Calluna shoots and Empetrum leaves	20	110	160	72	360	38	43	32	830	1300
Tö; July 1966; do.; do.	18	150	160	74	400	53	32	36	790	1300
Tö; Dec. 1966; do.; do.	19	88	170	72	350	29	29	36	790	1200
Tö; March 1967; do.; do.	30	63	150	79	320	47	33	37	800	1200
Sh; May 1966; Salici-Empetretum Lophoc.heter.subass.;										
Calluna shoots and Empetrum leaves	10	100	120	47	280	28	41	34	920	1300
Sh; July 1966; do.; do.	9	140	130	65	340	56	44	37	1000	1500
Sh; Dec. 1966; do.; do.	17	100	90	67	270	25	40	32	800	1200
Sh; May 1967; do.; do.	19	130	160	76	390	52	45	44	790	1300

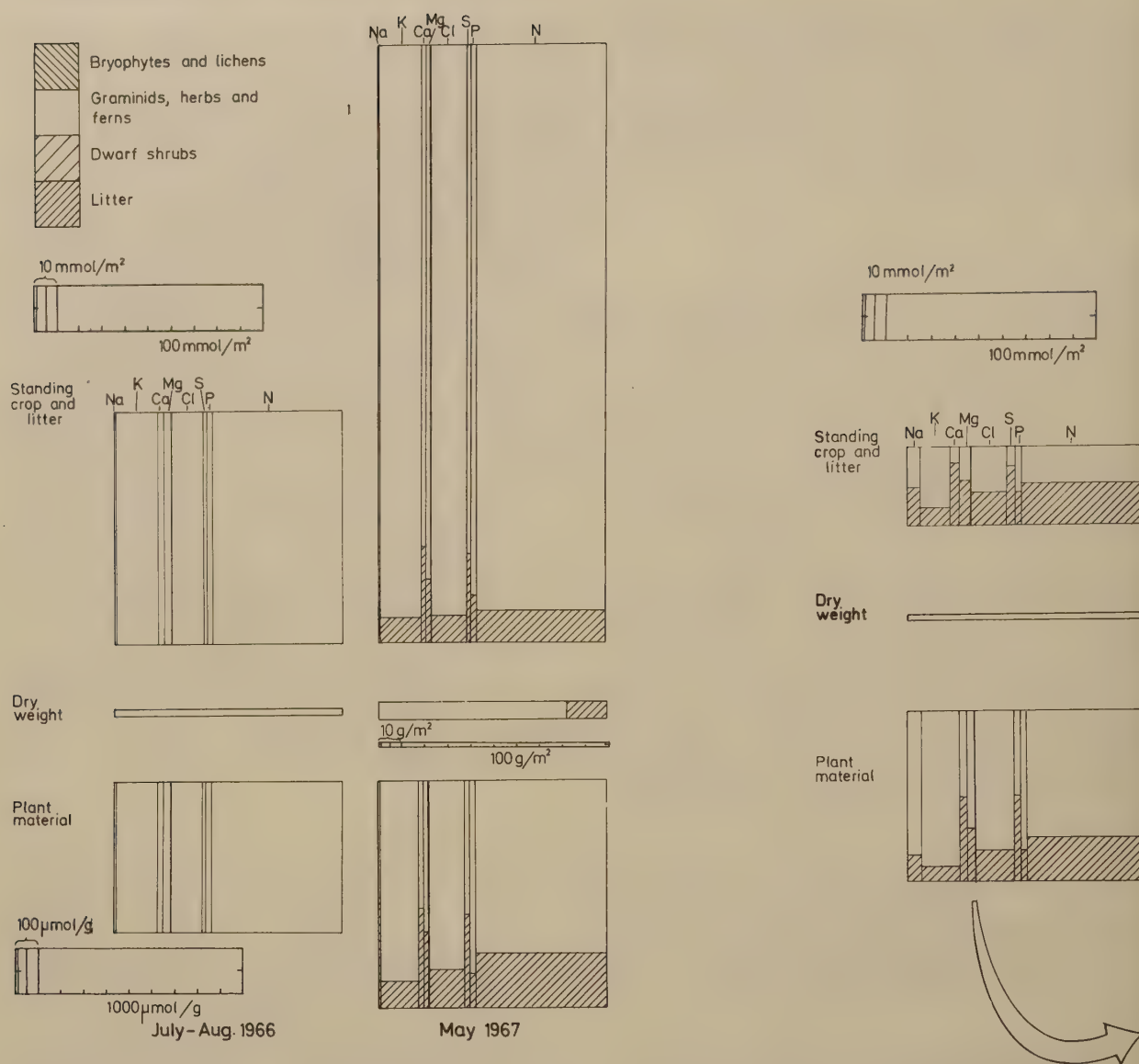


Fig. 79. Sandhammaren. Elymo-Ammophiletum typical subass. *Salsola kali* ssp. *kali* var. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 2, see Fig. 44; for scales, see Fig. 78. As indicated in the Fig., symbols are used in Figs. 78-91 to distinguish the four fractions.

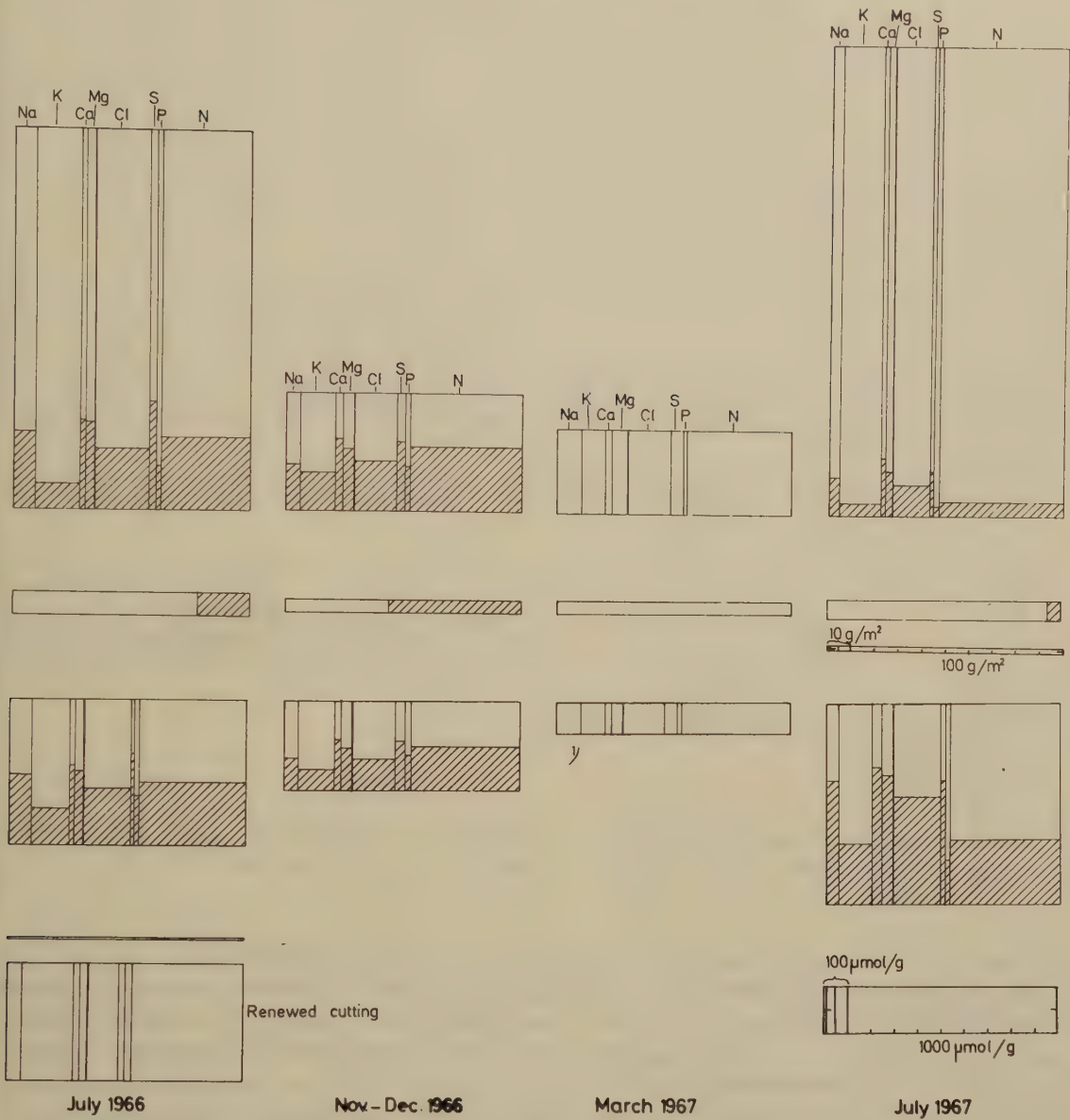


Fig. 80. Tönnersa. Elymo-Ammophiletum typical subass. Dry weight. Nutrients in plant material as well as in stand crop and litter. — Stand 3, see Fig. 43; for scales see Fig. 78; for symbols see Fig. 79.

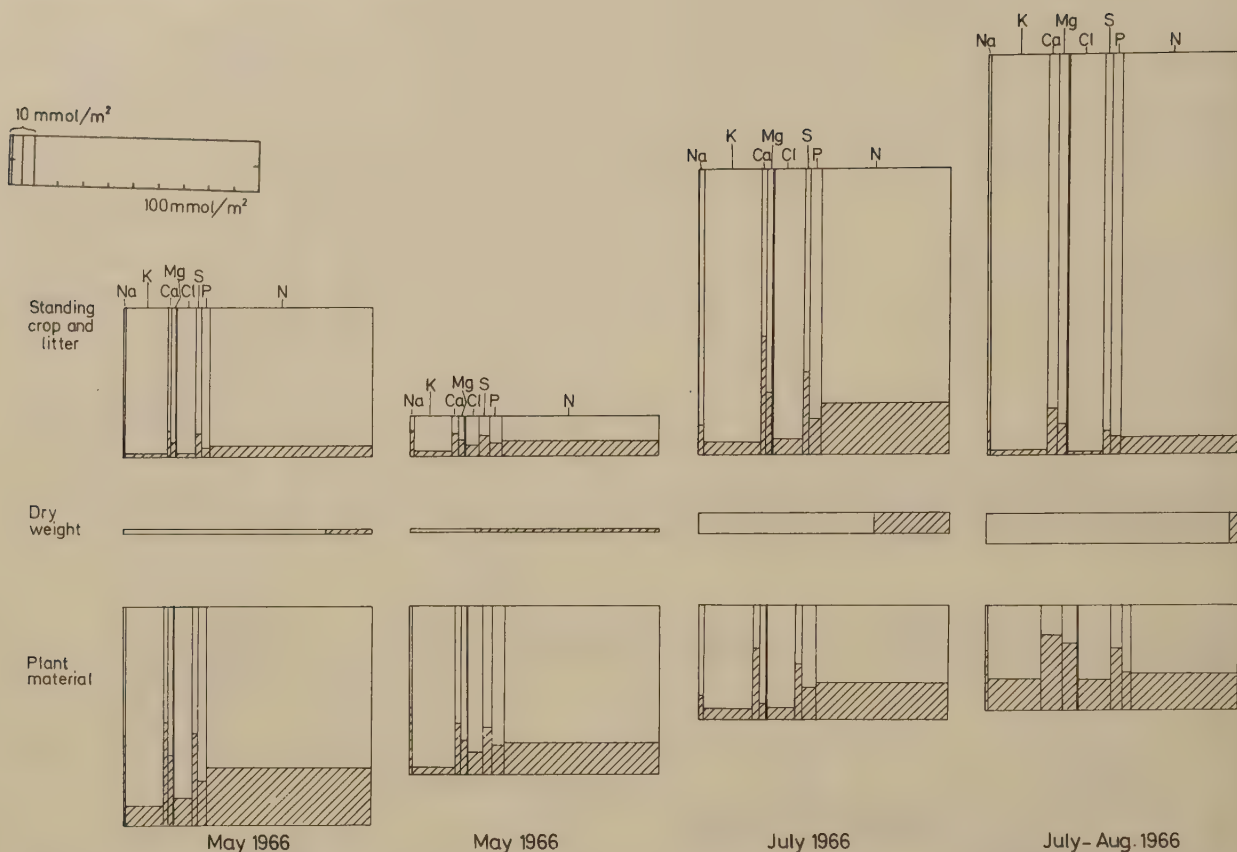


Fig. 81. Sandhammaren. Elymo-Ammophiletum typical subass. Dry weight. Nutrients in plant material as well as

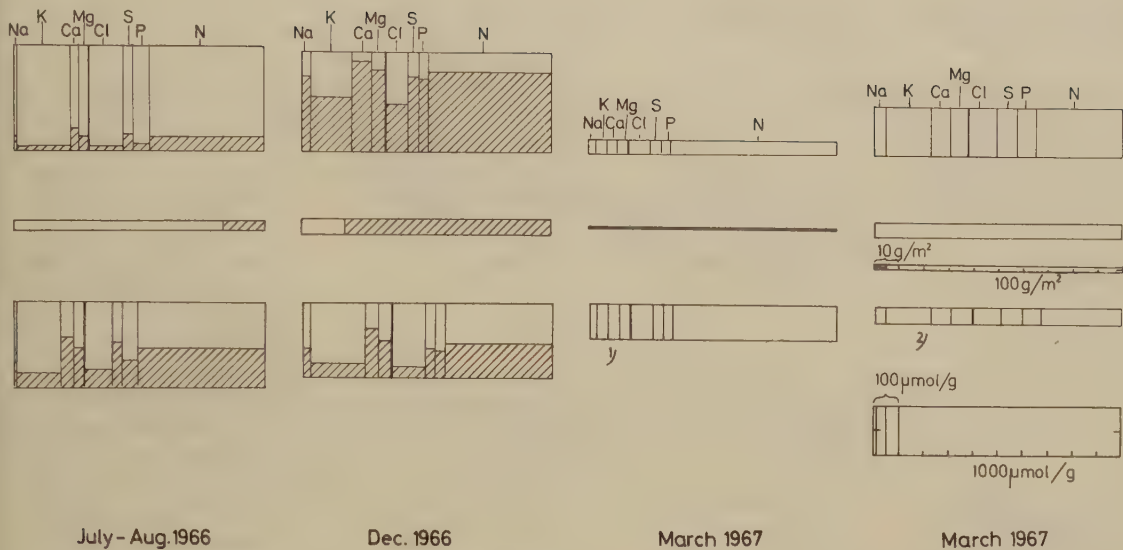
in standing crop and litter. — Stands 3-4, see Fig. 44; for scales, see Fig. 78; for symbols, see Fig. 79.

$K > Na > Mg > Ca$ at Tönnersa and $K > Ca > Mg > Na$ at Sandhammaren. K and Cl showed very small values in the litter (Figs. 82–83). The concentrations of S and P were about the same at Tönnersa, different from Sandhammaren, where P was always somewhat higher than S. The typical subassociation showed a seasonal decrease of plant nutrients. In *Hieracium umbellatum* ssp. subass. the decrease was only valid for some elements, e.g. K. The total sum of nutrients increased in the summer.

In the lichen-rich stands, *Violo-Corynephoretum* *Cladonia* subass. and *Cladonio-Corynephoretum*, the proportions of the nutrients were different. As a rule the metals were only one fifth or less of the determined constituents (Figs. 84–87). In *Cladonio-Corynephoretum* (stand 7) at Sandhammaren the metals were only one tenth (Fig. 87). The metal sequence was: $K > Na > Ca = Mg$ (Tönnersa) and $K > Ca > Mg > Na$ (Sandhammaren). The monovalent metals were predominant in the fraction with

living material. Especially Cl showed very low concentrations in the litter as well as in the bryophytes and lichens (ca. $10 \mu\text{mol/g}$). A deficiency of Cl may have severe effects on herbs and graminids (see Johnson et al. 1956 p. 352). N was dominant, often $> 2000 \mu\text{mol/g}$ N in the investigated stands and uniformly distributed in the three differentiated fractions. The non-metal sequence was: $N \gg Cl > P = S$ (Tönnersa) and $N \gg P = S > Cl$ (Sandhammaren). In *Corynephorus canescens* Rychnovská-Soudková (1961 p. 54) has found higher concentrations of N and K compared with Ca, Mg and P, which agrees with the proportions of the nutrients in the living fraction (Figs. 84–87).

In *Salicetum arenariae* *Ammophila arenaria* subass. the metals were about a third of all mineral components. The metal sequence was: $Ca > K > Mg > Na$. In the foliar part K exceeded Ca (Table 6). In birch leaves Holmen (1964 p. 199) has instead found higher concentrations of Ca than of K. In the winter



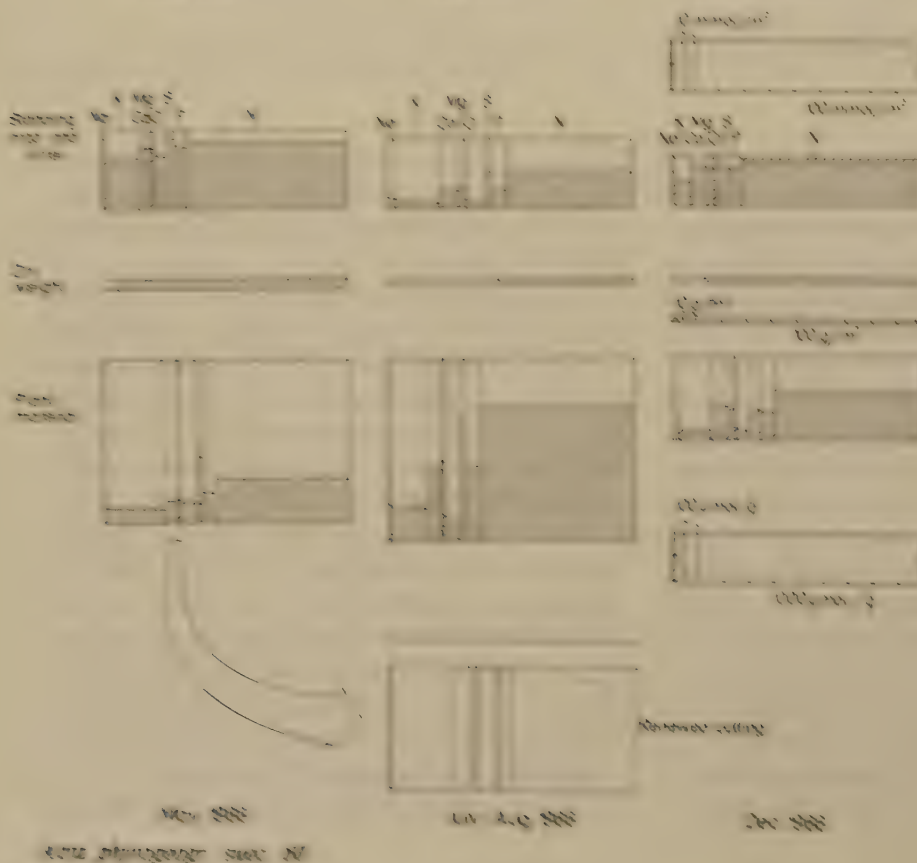
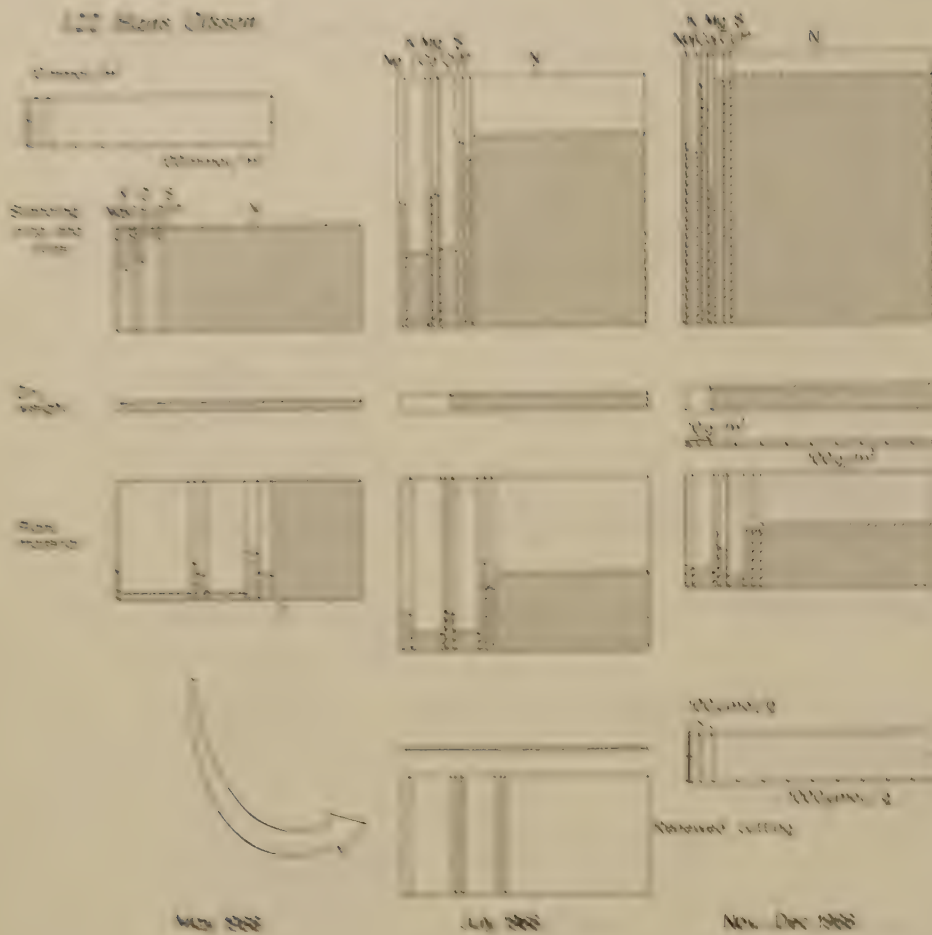
^{1, 2}The fractions graminids + litter are included.

a large part of the nutrients was accumulated in the litter (Fig. 88). There were 1100 µmol/g in the litter and 800 µmol/g in the nano-chamaephyte fraction. In July an investigation of the renewed standing crop from the stand cut in May was performed. K, Mg, S, P and N increased their concentrations (Fig. 88). In the foliar part K, Mg, Cl and S increased, while Na, Ca and P decreased. A translocation of Ca and Mg seems to occur. Ca is transported to the wood and Mg to the leaves. The S:N ratio agrees with that of herbs and graminids (see Dijkshorn & van Wijk 1967). In renewed standing crop of *Elymo-Ammophiletum* typical subassociation at Tönnersa S and P increased after cutting and Mg and Cl decreased (Fig. 80) in the living material. In *Hieracium umbellatum* ssp. subass. Na was higher and K, S and P had lower concentrations after cutting at Tönnersa. The reabsorbed concentrations of Ca and P (Fig. 83) were much higher at Sandhammaren (170 and 120 µmol/g respectively) than at

Tönnersa (50 and 60 µmol/g respectively). According to Wiersum (1961 pp. 62–69) the plants have ability to take up more P in a finer substratum, as at Sandhammaren.

In *Salici-Empetretum* the metals were about one third in *Festuca arenaria* subass., one fourth in *Lophocolea heterophylla* subass. at Tönnersa and one fifth at Sandhammaren, of all determined nutrients. The metal sequence was: K > Ca > Mg > Na (Figs. 89–91). In *Festuca arenaria* subass. the N content (Fig. 89) as well as the sum of the mineral elements was rather low. Also the sum of foliar nutrients was lower than that of *Lophocolea heterophylla* subass. (Table 6), where in four differentiated fractions S and P had similar concentrations and were much lower than the N quantities (Figs. 90–91). The amount of Ca was considerable in the wood. Tamm, C.O. (1953 p. 78) has indicated high Ca concentrations in old moss segments. The N content was evenly distributed among the fractions.

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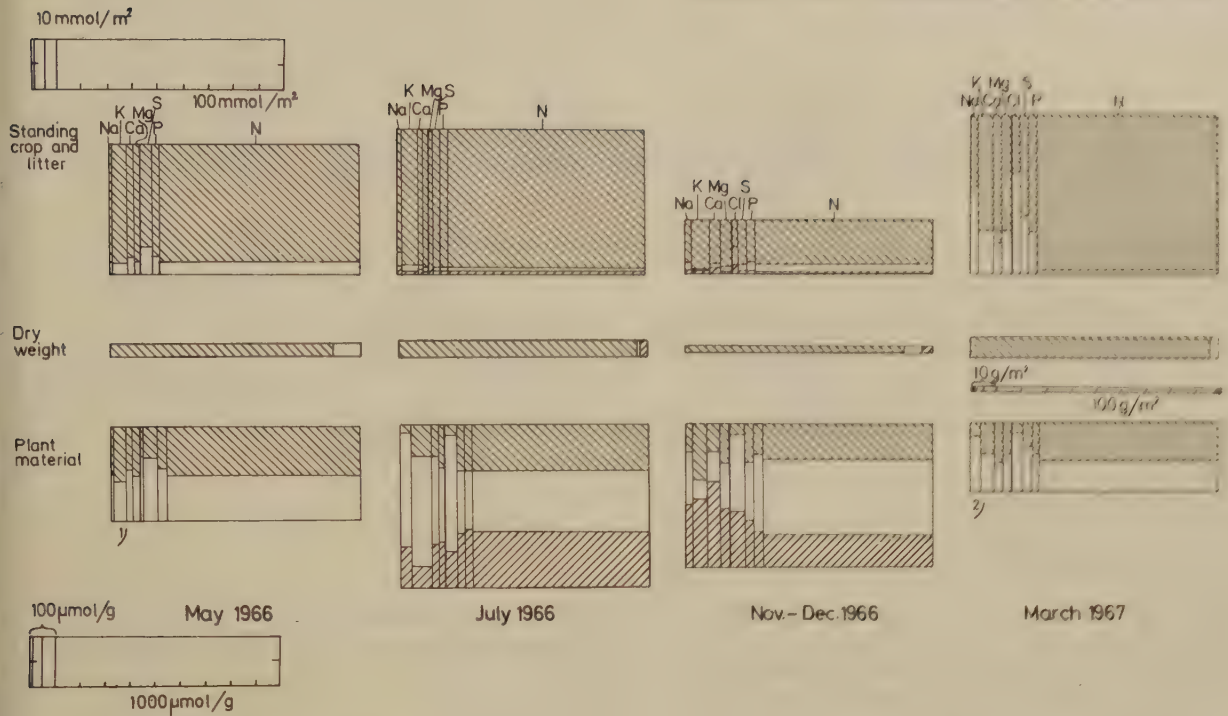


Fig. 84. Tönnersa. *Violo-Corynephorum Cladonia* subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 5, see Fig. 43; for scales,

see Fig. 78; for symbols, see Fig. 79.

^{1, 2}The fractions graminids + herbs and litter are included.

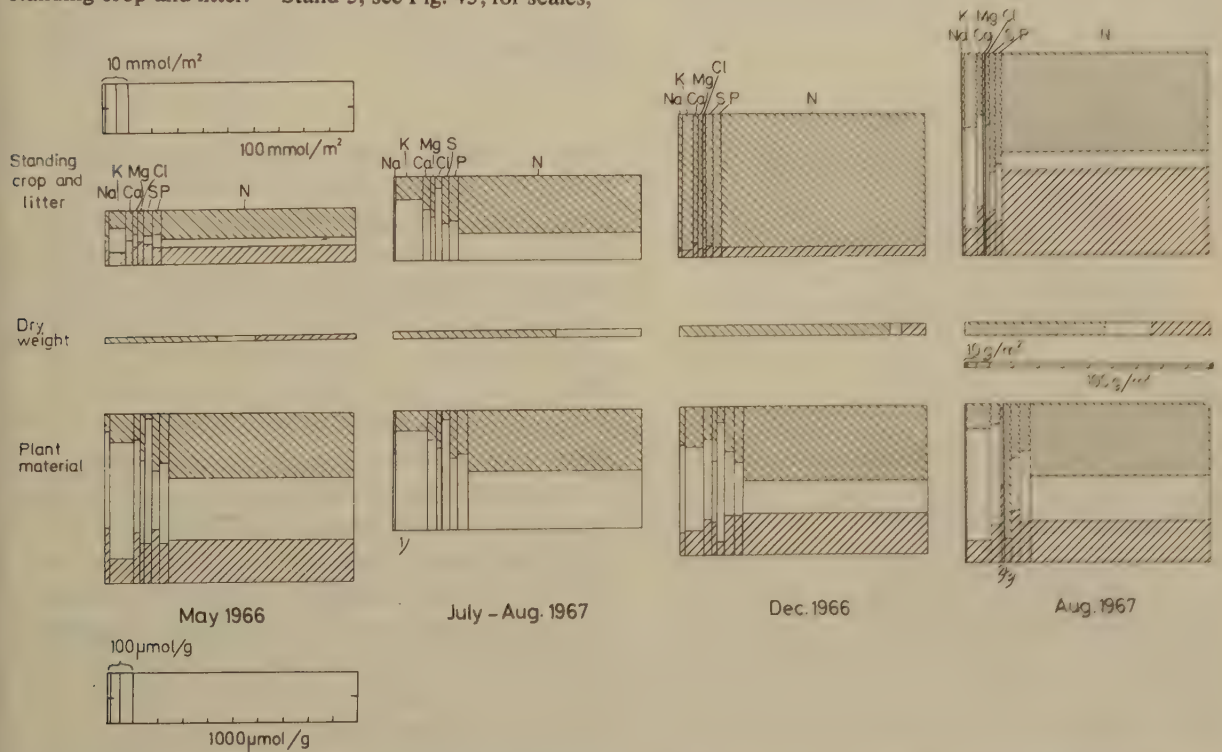


Fig. 85. Sandhammaren. *Violo-Corynephorum Cladonia* subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 6, see Fig. 44; for scales, see Fig. 78; for symbols, see Fig. 79.

¹The fractions graminids + herbs and litter are included.

²The value for Mg is lacking in the fraction graminids + herbs.

³The value for Cl is lacking in the fraction bryophytes + lichens.

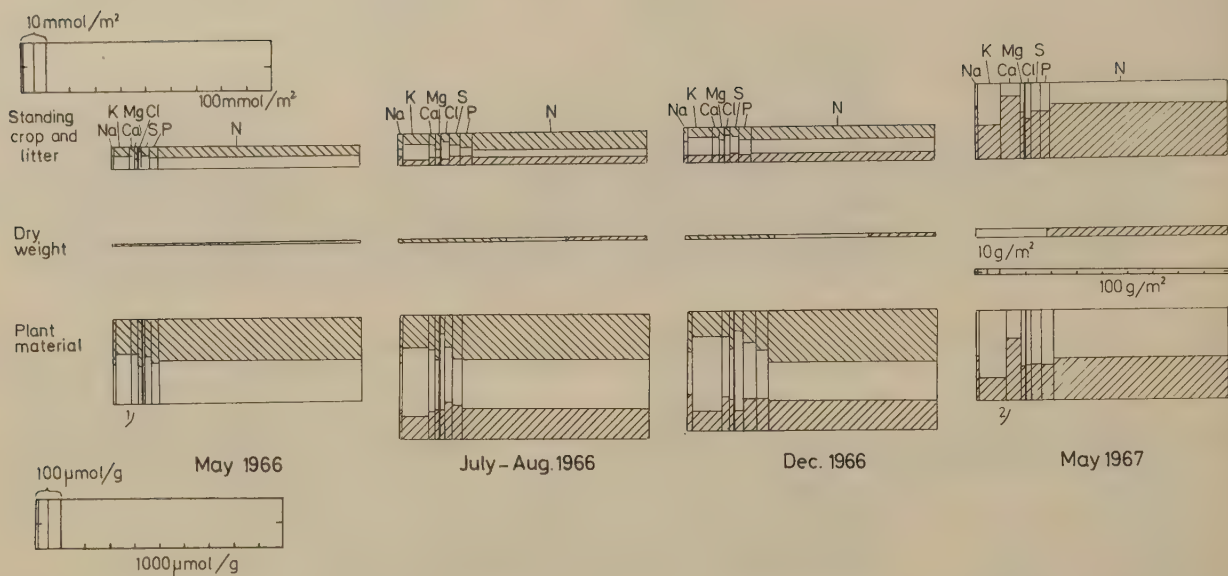


Fig. 86. Sandhammaren. Cladonio-Corynephoretum Cladonia subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 7, see Fig. 44; for scales, see Fig. 78; for symbols, see fig. 79.

¹The fractions graminids + herbs and litter are included.

²The fractions bryophytes + lichens and litter are included.

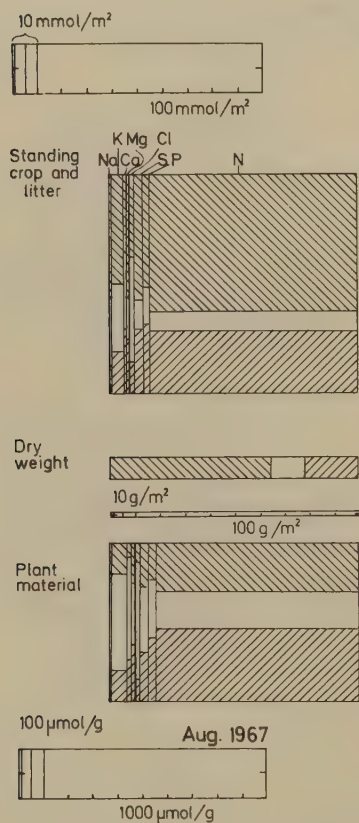


Fig. 87. Sandhammaren. Cladonio-Corynephoretum Cladonia subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 8, see Fig. 44; for scales, see Fig. 78; for symbols, see Fig. 79.

In the leaves of the nano-chamaephytes the metal sequence was somewhat different from that of the whole plant cover: $\text{Ca} = \text{K} > \text{Mg} > \text{Na}$. A similar order seems to occur in *Vaccinium myrtillus* (see Flower-Ellis 1971 p. 71).

Mineral nutrients in the standing crop and litter

In Honkenyetum peplodis at Tönnersa there was a strong increase in nutrients from May to July (Fig. 78). In the latter month the Na content here was the highest in the whole locality. The lowest concentration was found in *Salicetum arenariae*. The nutrient content in *Elymo-Ammophiletum Salsola kali* var. (Fig. 80) was about 1300 mmol/m² in July 1967. The litter fraction contained only a small amount of mineral constituents. In *Elymo-Ammophiletum* typical subass. the concentration of nutrients had a peak in the summer. Together with the increased uptake also some salt spray may have contributed (see Edwards & Claxton 1964 p. 262). The living fraction was predominant except in the winter and early spring (Figs. 80–81). At Tönnersa Na showed the lowest concentration in May, Ca in March. At Sandhammaren the Cl content was higher in the summer than in the winter. In *Elymo-Ammophiletum Hieracium* spp. subass. the total amount of nutrients was higher in the investigated stands at Tönnersa compared with those of Sandhammaren. Especially the portion of non-

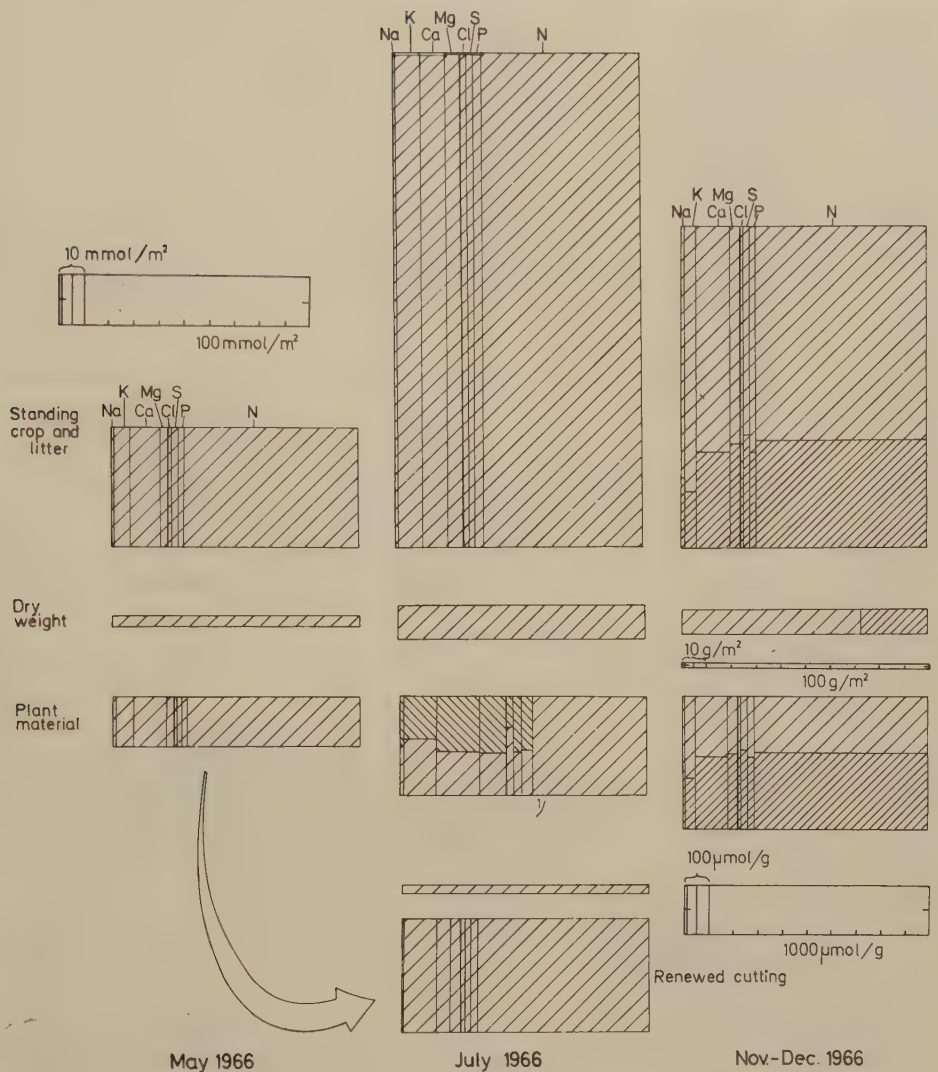


Fig. 88. Tönnersa. *Salicetum arenariae* *Ammophila arenaria* subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 6, see Fig. 43; for scales, see Fig. 78; for symbols, see Fig. 79.

¹The value for N is lacking in the fraction bryophytes + lichens.

metals was striking, mostly concentrated in the litter. In the lichen-rich vegetation the fractions litter as well as bryophytes and lichens contained much more nutrients than the part of living material of graminids and herbs. In *Cladonio-Corynephorretum* (stand 8) at Sandhammaren (Fig. 87) the contents in the three fractions were 230, 160 and 50 mmol/m² respectively.

In *Salicetum arenariae* the amount of nutrients had a peak in the summer (Fig. 88), about 1000 mmol/m². In *Salici-Empetretum Festuca arenaria* subass. there was also a pronounced peak in the summer, 490 mmol/m². In *Lophocolea heterophylla* subass. the situation in the plant cover was similar at

Tönnersa and Sandhammaren, except the high nutrient content of a sample from May on the latter locality. The nano-chamaephyte fraction was prevalent and contained 480 and 530 mmol/m² on the two localities. According to Mork (1946 Table 7, 12) Ca comes after N in concentration, and according to Robertson & Davies (1965) and Chapman, S.B. (1967 p. 684) K is somewhat higher than Ca in the above ground phytomass, which agrees with the present results. From the researches of Tyler et al. (1973 Table 2) there are about 20.5 kg/ha K and 19.5 in the above ground biomass of a *Calluna* ecosystem and 15.4 and 11.4 respectively of an *Erica* ecosystem on the wet heath Skanör's Ljung.

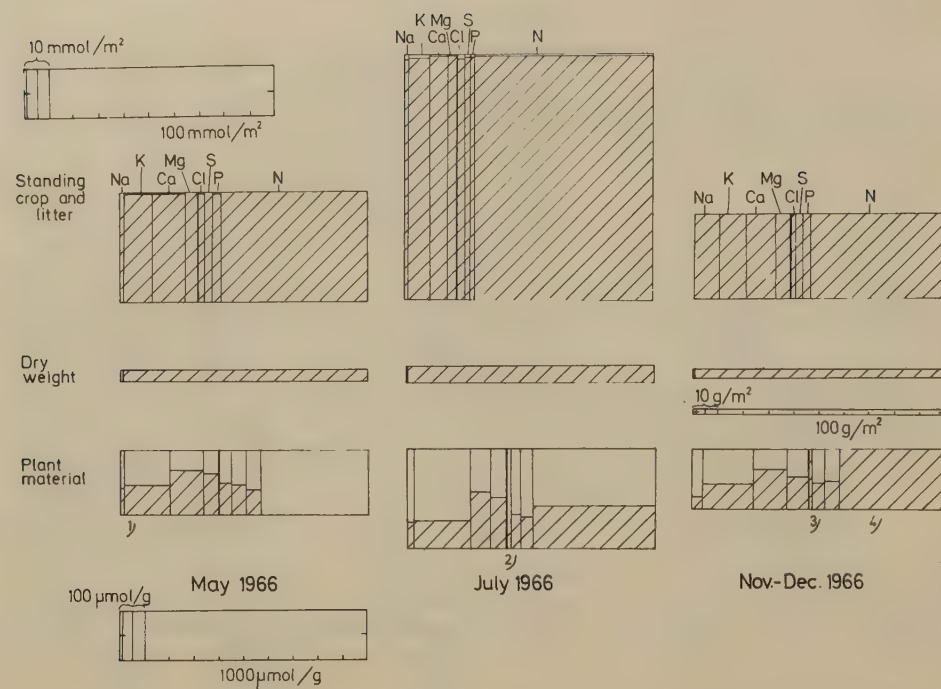


Fig. 89. Tönnersa. Salici-Empetretum *Festuca arenaria* subass. Dry weight. Nutrients in plant material as well as in standing crop and lichens. — Stand 8, see Fig. 43; for scales, see Fig. 78; for symbols, see Fig. 79.

^{1,4}The value for N is lacking in the fraction graminids + herbs.

^{2,3}The value for Cl is lacking in the fraction graminids + herbs.

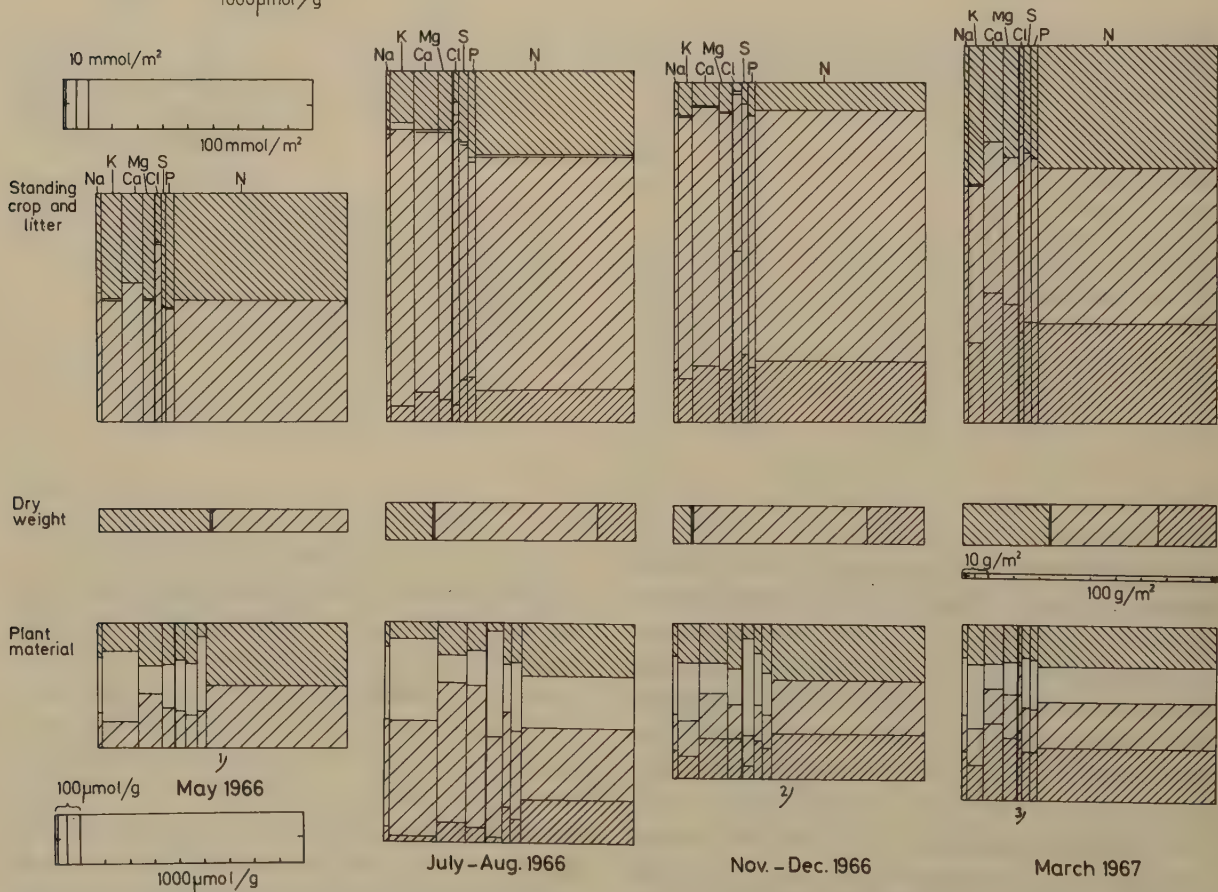


Fig. 90. Tönnersa. Salici-Empetretum *Lophocolea heterophylla* subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 9, see Fig. 43; for scales, see Fig. 78; for symbols, see Fig. 79.

^{1,2}The value for N is lacking in the fraction graminids + herbs.

³The value for Cl is lacking in the fraction graminids + herbs.

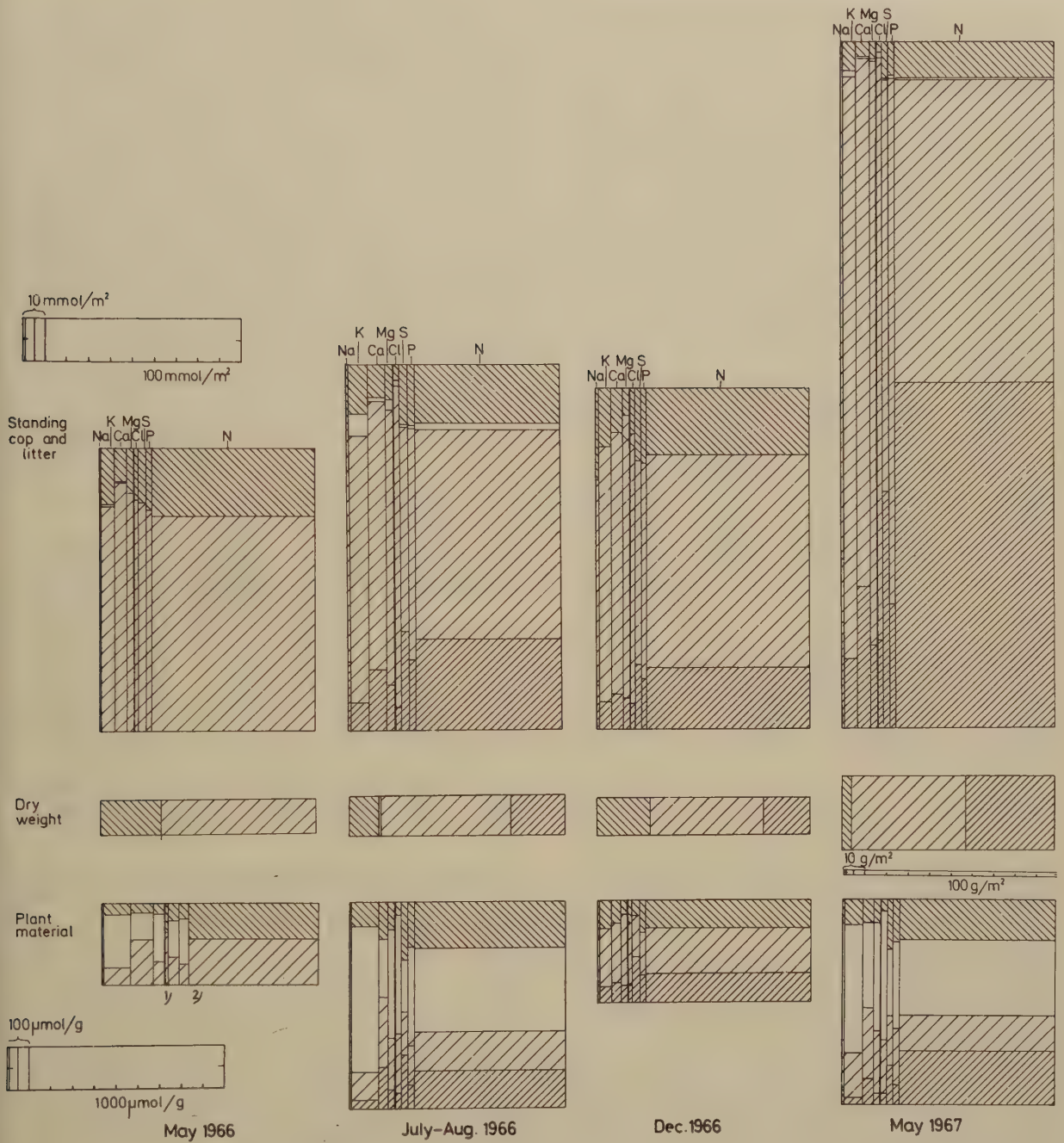


Fig. 91. Sandhammaren. Salici-Empetretum Lophocolea heterophylla subass. Dry weight. Nutrients in plant material as well as in standing crop and litter. — Stand 9, see Fig. 44; for scales, see Fig. 78; for symbols, see Fig. 79.

¹The value for Cl is lacking in the fraction graminids + herbs.

²The value for N is lacking in the fraction graminids + herbs.

Soil — plant relationships

The available nutrients in the soil were recorded down to 1 m (Table 7) but in the Figs. 92 and 93 were calculated to be comparable with the plant nutrients expressed as mmol/m². The storage nutrients (Table 8) are given in mg/g and % of the total amount of oxides. The uptake of mineral elements by the vegetation occurs in several stages counteracted by ion competition (Lotse 1963 p. 131). At Tönnersa there were higher amounts of Ca in the plant cover compared with Sandhammaren, where the contents of available Ca and P in the soil were more evident (Figs. 92 and 93). More K was found in the plant cover than in the soil. K is according to Sjörs (1954 p. 108) strongly absorbed in living plants contrary to Ca, more accumulated in soil organic substance. The amounts of Na and Cl were increased in the seaward stands. In the lichen-rich stands there were small concentrations of

nutrients in both vegetation and soil. According to Rychnovská-Soudková (1961 p. 54) *Corynephorus canescens* can take up higher quantities of K and P than of Ca and Mg. K supplied with the salt spray compensates for the leaching (Etherington 1967 p. 750). According to Willis & Yemm (1961) the deficiency in N, P and K could, in several cases, lead to an open dune vegetation. A supply of these nutrients (Willis 1963) closes the plant cover. The available amounts of NH₄⁺ and NO₃⁻ in the soil are extremely low; only about 0.01–0.04 mmol/dm³ were measured. Also total N (Table 8) showed low values in the mineral soil. In humus-rich stands in the dune depressions the quantities were obviously increased. The sum of all determined nutrients is higher in the plant cover at Tönnersa than at Sandhammaren, where the sum of available nutrients in the soil is greater.

Considering the two localities as maritime ecosystems, an average of the dry weight and of the

Table 7. Water content, loss on ignition (kg/m³) and soil nutrients (mmol/m³) extractable in 0.5 M acetic acid, down to 1 m depth. Average of the stands 1-9, July-August 1966.

locality	water content	loss on ign.	Na	K	Ca	Mg	metals, total	Cl	S	P	elements, total
Tönnersa	82	4.7	640	370	1300	580	2900	430	170	410	3900
Sandhammaren	120	3.0	590	250	2800	420	4100	280	220	1700	6300

Table 8. Elementary composition (mg/g and % as oxides) calculated on ignited soil (N mg/g of dry weight). Average from the stands at various depths (cm).

locality; stand no.; depth in cm	mg/g										d.w. N
	Al	Fe	Ti	Ca	Mg	Na	K	Mn	S	P	
1. Tö; 1-6, 8-9; 0-10	35	8.6	3.6	8.5	1.4	14.0	22.0	0.5	1.1	0.09	0.21
2 Tö; moist humus-rich stand; 0-10	38	7.4	2.0	7.4	1.4	15.0	23.0	0.3	0.5	0.07	0.93
3 Tö; 1-9; 50-60	22	4.9	1.5	2.2	0.4	6.3	15.0	0.4	0.1	0.06	0.03
4 Sh; 1-7, 9; 0-10	14	2.5	1.1	2.6	0.4	4.9	10.0	0.1	0.5	0.09	0.18
5 Sh; moist humus-rich stand; 0-10	14	3.5	1.8	3.0	0.5	3.6	7.1	0.1	2.7	0.17	7.40
6 Sh; 1-9; 50-60	14	1.8	0.7	1.1	0.2	3.7	10.0	0.1	0.1	0.12	0.04

locality	% as oxides										
	SiO ₂	Al ₂ O ₃	Fe ₂ O ₃	TiO ₂	CaO	MgO	Na ₂ O	K ₂ O	MnO	SO ₃	P ₂ O ₅
1 Tö	72.8	13.3	2.5	0.6	1.2	0.2	3.8	5.3	0.1	0.3	<0.1
2 Tö	72.2	14.4	2.1	0.3	1.1	0.2	4.0	5.5	<0.1	0.1	<0.1
3 Tö	84.3	8.3	1.4	0.3	0.3	0.1	1.7	3.6	0.1	<0.1	<0.1
4 Sh	89.5	5.3	0.7	0.2	0.4	0.1	1.3	2.4	<0.1	0.1	<0.1
5 Sh	89.5	5.3	1.0	0.3	0.4	0.1	1.0	1.7	<0.1	0.7	0.1
6 Sh	90.4	5.3	0.5	0.1	0.2	<0.1	1.0	2.4	<0.1	<0.1	0.1

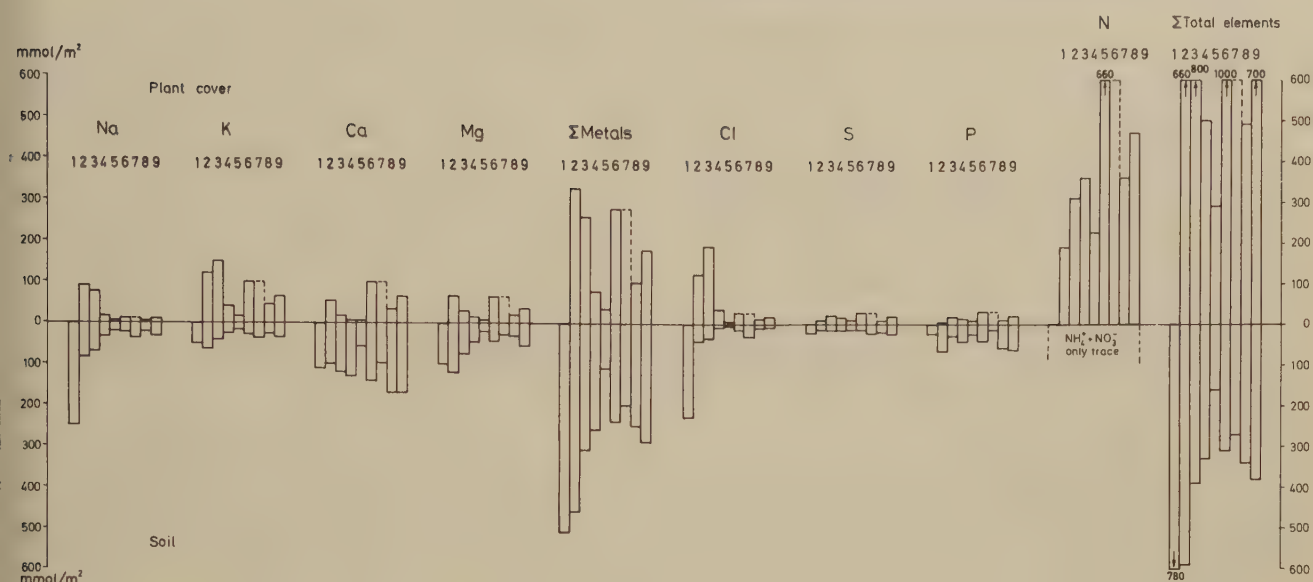


Fig. 92. Tönnersa. July-August 1966. Mineral nutrients in plant cover and soil (one tenth of a cubic metre). — Stands 1-9, see Fig. 43.



Fig. 93. Sandhammaren. July - August 1966. Mineral nutrients in plant cover and soil (one tenth of a cubic metre). — Stands 1-9, see Fig. 44.

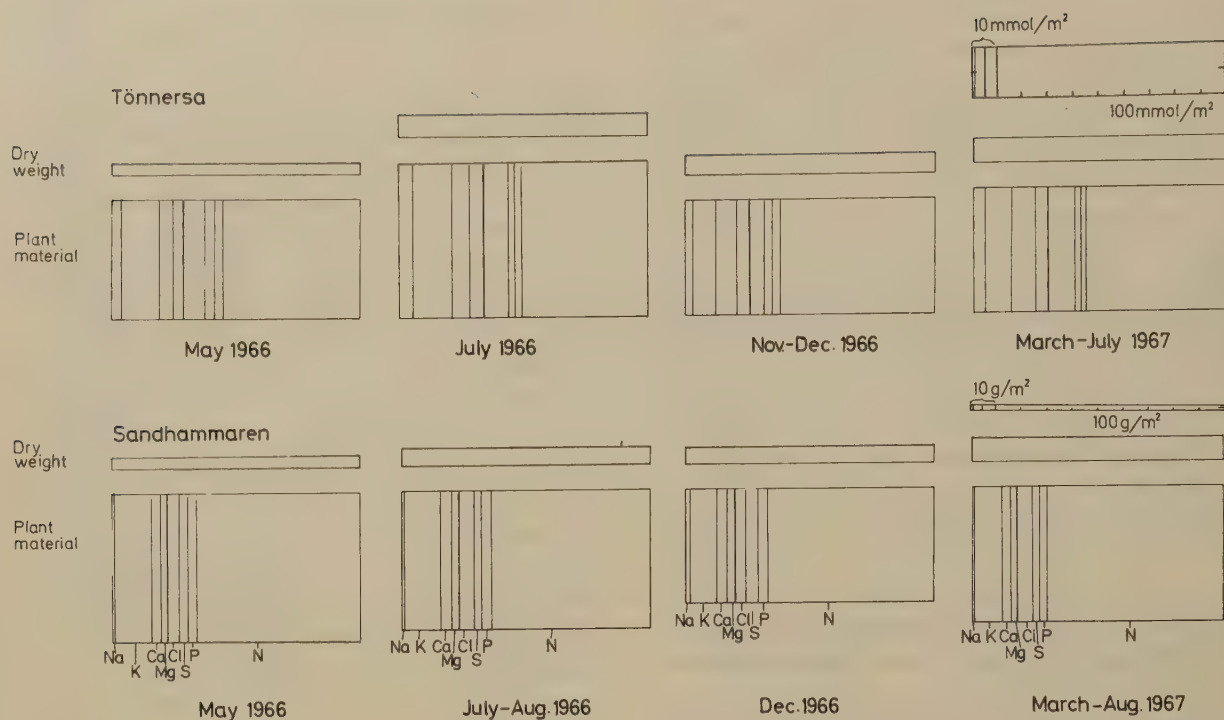


Fig. 94. Average of dry weight and nutrients in plant material of all investigated stands at Tönnersa and

Sandhammaren arranged into four groups. — For scales, see Fig. 78.

nutrients in the plant material are estimated for all investigated stands included (Fig. 94) and arranged into four groups during the season. The groups of Tönnersa are similar to those of Sandhammaren. The lowest concentrations of nutrients were found in the winter. The concentrations of metals were greater at Tönnersa than at Sandhammaren. As seen in Tables 7 and 8 the composition of available nutrients and storage mineral elements is much different between the two localities. Only Ca, S and P had higher concentrations at Sandhammaren, but the total quantity of nutrients was much higher compared with Tönnersa. At the latter locality all storage nutrients exceeded the corresponding at Sandhammaren, where the content of SiO_2 (calculated as the difference between 100 % and the sum of all measured oxides) was higher. Al_2O_3 was ca. 14 % at Tönnersa and only 5 % at Sandhammaren. At both localities the following metal sequence is valid: $\text{Si} > \text{Al} > \text{K} > \text{Na} > \text{Fe} > \text{Ca} > \text{Ti}$. All elements had higher concentrations at Tönnersa, where the amounts of K was just above 20 mg/g, than at Sandhammaren (K ca. 10 mg/g). Only in the humus-rich substratum in the dune depressions at the last-mentioned locality S, P and N had higher values

than at Tönnersa. Most constituents, except Al, K, Mn and P at Sandhammaren, showed lower amounts at the depth of 50–60 cm than in the surface soil.

Surface water

The humus interference

Analyses on untreated water samples (a), have been checked with analyses after digestion (b). K, Mg and Na show no change in concentration. The Ca values have increased somewhat after digestion. S has furthermore been determined on samples treated with active carbon (c). An average of 4 samples from the wide dune depression at Tönnersa indicate the following concentrations (mmol/l): (a) 0.35, (b) 0.36, (c) 0.12. An average of 7 samples from a dune depression at Sandhammaren shows: (a) 0.15, (b) 0.11, (c) 0.02. The decrease in concentration after treatment with active carbon is obvious. At Sandhammaren the water is stagnant for a long period, brownish and rich in colloids and that is the explanation of the low result after treatment with active carbon which has a strong adsorption effect on

Table 9. pH and mineral nutrients (mmol/l) in the surface water. Average of the water samples.

locality; site; number of samples	pH	Na	K	Ca	Mg	Cl	S	P	Ca/Mg	Na/Cl	K/Ca
Tö; sea; 7	7.5±0.3	160±37	3.7±0.6	3.5±0.7	19±4	200±43	11±5	0.002	0.2	0.8	1.1
Tö; river Genevadsån; 5	7.0±0.3	0.38±0.08	0.05±0.02	0.17±0.09	0.11±0.05	0.48±0.44	0.17±0.03	0.001	1.6	0.8	0.3
Tö; small dune depr.; 1	7.0	0.69	0.13	0.21	0.18	0.89	0.30	0.001	1.2	0.8	0.6
Tö; wide dune depr.; 6	6.4±0.3	0.99±0.27	0.12±0.05	0.32±0.13	0.19±0.02	1.1±0.48	0.31±0.12	0.002	1.7	0.9	0.4
Sh; sea; 8	7.7±0.2	94±7	2.4±0.3	2.5±0.2	11±0.7	120±6	6.7±1.0	0.001	0.2	0.8	1.0
Sh; dune depr.; 4	5.2±0.7	0.24±0.04	0.03±0	0.06±0.03	0.07±0.02	0.21±0.10	0.18±0.04	0.008	0.9	1.1	0.5
Sh; dune depr.; 5	5.0±0.6	0.29±0.04	0.03±0	0.08±0.06	0.08±0	0.37±0.05	0.15±0.01	0.005	1.0	0.8	0.4

the colloids in the water. The S concentration was much lower at Sandhammaren, where also the S adsorption was stronger than at Tönnersa.

Distribution of pH and mineral nutrients

In the sea water just near the beach the pH was about 7.7, in the small river Genevadsån ca. 7.0, in the dune depressions at Tönnersa 6.2–6.9 and at Sandhammaren 4.3–5.9. The last-mentioned locality showed also a more acid substratum and pH measured directly in the peaty humus was lower than in the water (see Persson, Å. 1962 p. 77). From various South Swedish lakes Malmer (1961) has reported a pH ca. 6, in mire sites 3.7–6.5 (Malmer 1962 b p. 29). In calcareous English dune slacks the pH is about 8 (Gorham 1961). In the dune depressions the pH had decreased in the summer. According to Malmer (op.cit. p. 24) a decrease of the free water volume leads to a reduction of pH and a dilution through precipitation or inundation to an increase.

The relative concentrations of the measured ions in the sea water agree with the composition of a standard sea water (see Dyrssen 1966 pp. 280–281).

The ion concentrations were much higher at Tönnersa than at Sandhammaren (Table 9). Na and Cl were about 10 times as high as Mg and S. The values of K and Ca were similar. All determined constituents showed very low concentrations in the water of the small river Genevadsån. In the wide dune depression at Tönnersa the amounts of Na and Cl were as high as 1 mmol/l, in the adjacent small seaward depression lower (Table 9). If the surface water is rich in colloids the Ca content increases. All mineral elements in the depressions at Tönnersa had higher concentrations compared with those of the river in the vicinity. Except P all determined nutrients in the depressions at Sandhammaren had lower values compared with Tönnersa. The ion condition at Sandhammaren seems to be more related to the corresponding situation in poor mire water (see Malmer op.cit. p. 53). The cation sequence in the sea water is: Na > Mg > Ca = K. The sequence in the fresh water is: Na > Ca = Mg > K. The Ca/Mg ratio in fresh water was 1.2–1.7 at Tönnersa and 0.8–1.0 at Sandhammaren. The Na/Cl ratio was about 0.8 for both localities (Table 9). The K/Ca ratio was more variable, often below 0.5.

Summary

In an introductory chapter the investigation is presented and illustrated in a hypothetical quadrant system. In the section on Topography and geology the Quaternary sand deposits are briefly dealt with, and types of coast are described. The mean annual temperature is 7–8°C. The yearly precipitation is low, with a maximum in July–August, but much higher in the inland than along the coast, where the climate is comparatively sunny and dry. The vegetation period is about 180 days with > 6°C. As a rule the accumulative (positive) sand transport occurs during spring and summer, the erosive (negative) one during autumn and winter. Miniature barchans may be seen on the beaches. At Tönnersa small parabola dunes have increased in later years. At Sandhammaren and Furuboda there are dune rows parallel to the shore line. The beach bar at Tönnersa and the south spit of the Falsterbo peninsula are examples of marine accumulation with rapid changes.

In recent time the landscape and the forest composition has been influenced by grazing, felling, burning and haymaking. The dwarf shrub heaths have decreased and partly been afforested. The investigation areas are situated in the south-Scandinavian deciduous forest region with oak and beech, which is connected with the West and Central European vegetation. Man and domestic animals have influenced the sands since the Neolithic period. Generally the sands started to shift in historic time. From the beginning of the 16th century documents record the sand shifting. Deciduous forests have probably been destroyed and the vegetation burnt on several localities. Later many sites were planted with marram grass or pine. The first action from the government to stop the sand from blowing is reported from Ängelholm in 1739. Methodical pine afforestation started in the first part of the 19th century, but at Sandhammaren the first pine stand dates from 1760. However, the mobile sand was not controlled there until the 20th century. The sand vegetation decreased in area and the arable land increased. Nowadays human activity has given rise to new erosion problems.

Many aspects of the sands are given in the literature. The economic attitude of the Linnean era was continued by promotion of planting of pine and research in forestry. Many authors have treated parts of the vegetation in a phytogeographical or phytosociological way, or given examples of vegetational changes. In the past decade papers concerning questions of nature conservancy have been published. Related disciplines such as zoology, geology and physical geography, as well as history of rural economy, are also represented by many scientific contributions.

The number of plants has remained fairly constant during the last two centuries as is evident from old flora lists. The flora elements, as well as changes in the distribution of some plants, are discussed with regard to arrangement in the quadrant system referred to above. A list of selected taxa with special qualities, such as morphology, ecology and distribution, is presented for vascular plants as well as bryophytes and lichens, in particular the genus *Cladonia*.

The phytosociological methods are those proposed by Du Rietz, G.E. (1957), as a whole agreeing with the Braun-Blanquet system. The vegetational analysis, following Malmer (1962), stresses mainly the floristic composition, in certain cases with stronger consideration of the physiognomy. The soil studies include pH, loss on ignition, grain size as well as the stratification of the soil type (see also the last part).

The present study of the vegetation represents a synthesis of floristic and ecological features encountered in a phytogeographically important transitional area, within the Scandinavian outlier of the Nemoral zone (Sjörs 1963 and 1971) of Western and Central Europe, but very close to the boreo-Nemoral zone.

A great number, 36, of plant communities have been investigated and placed into a detailed phytosociological system (Passarge & Hofmann 1968, Géhu & Géhu 1969, Westhoff & Den Held 1969). Some of the plant communities have not been described earlier. The descriptions deal with classification, structure, development, ecological remarks, distribution and sociological relationships.

A survey of the sociological classification is given in Table 3.

Annual *drift vegetation*, *Cakiletea maritimae*, contains halo-nitrophilic therophytes of *Atriplicetum littoralis* and *Cakiletum maritimae*. Perennial drift vegetation, *Agropyretea pungentis*, has also halo-nitrophilic hemicryptophytes. *Honkenyetum peploidis* is a specialized association belonging to the alliance *Honkenyo-Crambion maritimae*, whereas *Honkenyo-Agropyretum acuti*, often with *Elymus arenarius* as a dominant, and *Lepidietum latifolii*, with a less halophilic tendency, both belong to the alliance *Agropyrrion pungentis*.

The *marram and sandy grassland vegetation* contains various ecosystem on immature soils with a thin humus layer. The pure marram grass vegetation, *Ammophiletea*, is dependent on a continuous sand accretion. In South Sweden this class is represented by *Elymo-Ammophiletum* which is dominated by hemicryptophyte-graminids and according to a new interpretation one of four vicariant associations. *Elymo-Ammophiletum* has been subdivided into a typical subassociation, a

Hieracium umbellatum ssp. subass. and an *Ammophila arenaria* soc. Of an anthropogenous origin is a nitrophilic inland lyme grass vegetation, *Artemisietea vulgaris*, with a *Berteroa incana* - *Elymus arenarius* comm. which is not similar to the xerophilic *Elymus arenarius* stands in some places in East Scania.

The *short, dry grassland vegetation* is chiefly composed of Koelerio-Corynephoretea. The first order Corynephoralia is represented by a pioneer Cladonio (dstrictae) -Corynephorum which occurs only in small fragments and seems to die away as a consequence of the closing of the sand vegetation. A typical subassociation, often considered as a *Corynephorus canescens* soc., and a *Cladonia* subass. have been separated. In the second order, *Festuco-Sedetalia*, four plant communities have been studied. *Violo-Corynephorum* consists of hemicryptophytes and therophytes. In normal successions *Ammophila arenaria* is still present. The association is split into a typical subassociation and a *Cladonia* subass. *Teesdalia-Corynephorum* grows on dry, inland, glaci-fluvial sands with *Cladonia glauca*, *C. degenerans* and *C. verticillata* as differential taxa towards the previously mentioned coastal association. A typical sub-association and an *Artemisia campestris* subass. with several variants are found. *Pleurozium schreberi* - *Agrostis tenuis* comm. is only found at Ängelholm. In certain stands *Deschampsia flexuosa* is a dominant, in others *Carex arenaria*. Finally, *Antherico-Koelerietum glaucae* is rich in therophytes, both summer and winter annuals. A typical, moss-rich subass. and a *Cladonia* subass. occur.

A *poor meadow vegetation*, Arrhenatheretea, is represented by a *Festuca ovina* - *Rumex acetosa* comm., mainly on verges and margin pastures.

The *dwarf shrub and bush vegetation* includes true dwarf shrub vegetation, *Nardo-Callunetea*, which consists of four associations. *Salicetum arenariae* is a specialized association with *Salix arenaria* as a characteristic dominant. An *Ammophila arenaria* subass. and a *Carex nigra* subass., have been distinguished. *Salici-Empetretum* consists of different chamaephytes in closed or even dense stands, normally forming ranker soils. The floristic differentiation is into *Empetrum nigrum* soc., *Festuca arenaria* subass., *Polypodium vulgare* subass., and *Lophocolea heterophylla* subass., the latter often with seedlings of pine and birch. A *Calluna vulgaris* soc. is probably a part of the association *Cladonio-Callunetum* which lacks characteristic and differential taxa. The soil type is a podsol. Finally, *Agrostio-Callunetum* has a group of thermophytes as differential taxa towards other dwarf shrub vegetation. It occurs mainly inland on glaci-fluvial sands.

Of a different origin is an anthropogenous *rose bush vegetation* along the west coast developed as an *Agropyro-Rosetum rugosae* belonging to *Urtico-Sambucetea*. The *bog myrtle vegetation*, *Molinio-Myricetum gale*, belongs to the *Betulo-Franguletea* and forms pioneer stands in moist meso- or oligotrophic habitats. A coastal *Salix arenaria* subass. contains five variants along a hydro-gradient. It is different from an inland, typical subass. The *Molinia coerulea* soc. has a

tussocky physiognomy.

The *forest and shrubby wood vegetation* is dominated by pine, oak, alder and birch. The *pine vegetation*, part of the *Vaccinio-Piceetea*, consists of *Cladonio-Pinetum sylvestris* on podsol or podsol-ranker. It is subdivided into a typical subass. with *Cladonia rangiferina* and a *Corynephorus canescens* subass. *Vaccinio-Pinetum sylvestris* is normally triple-layered and has an A-B-C-soil profile with well-developed raw humus. It can be divided into an *Empetrum nigrum* subass. (different from the inland, typical subass.) and a *Quercus petraea* subass. In a *Deschampsia flexuosa* - *Pinus sylvestris* comm. *Deschampsia flexuosa* as well as various bryophytes are important in the undergrowth. The soil has a thick raw humus layer.

The *oak vegetation*, *Deschampsio-Quercetea robori-petraeae*, has been divided into four plant communities. A shrubby *Agrostis tenuis* - *Populus tremula* comm. with *Populus tremula* growing as a nanophanerophyte forms acidophilic stands with some relationship to *Betulo-Franguletea*. An *Oxalis acetosella* - *Quercus petraea* comm. contains two phanerophyte layers, an upper with *Quercus petraea* and a lower with *Sorbus aucuparia*. The soil profile is considered a podsoloid. *Melampyro-Quercetum roboris* occurs as its *Calamagrostis epigeios* vicariant, separable from an inland vicariant, and contains various acidophytes such as *Convallaria majalis* and *Deschampsia flexuosa*. The podsol is much more distinct in the inland vicariant than in the coastal one. A typical subass. with a pine variant, a *Corynephorus canescens* subass., and a *Corylus avellana* subass. have been distinguished. A mesophilic *Agrostio-Quercetum roboris*, characterized by a group of differential taxa, occurs mainly on glaci-fluvial sand, often as park-like stands. The soil profile is a weakly developed podsol or a podsoloid.

The *alder vegetation* is divided into an alder carr and an alder meadow vegetation. The former, *Carici-Alnetea glutinosae*, is represented by *Irido-Alnetum glutinosae*. It is a triple or quadruple-layered vegetation differentiated into a *Potentilla palustris* subass. and a *Mnium punctatum* subass. in mesotrophic habitats. The alder meadow vegetation, *Geranio-Fraxinetea excelsioris* is present as *Filipendulo-Alnetum glutinosae*, with several mesophytes including *Anemone nemorosa* dominant in spring. Here the soil profile is a pseudogley. The birchwoods include a *birch heath vegetation* and a *birch fen vegetation* both within *Molinio-Betuletea pubescentis*. The former, *Myrico-Betuletum pubescentis*, occurs on acid, moist sandy soils. The latter, *Polytricho-Betuletum pubescentis*, occurs in depressions with an anmoor or peaty fen soil.

Sandy wetland vegetation comprises low vegetation, marsh vegetation and aquatic vegetation. The *low vegetation* has three plant communities, viz., a *Carex nigra* - *Calamagrostis epigeios* comm. on moist sand, a *Carex rostrata* - *Juncus effusus* comm., which has a poor/rich gradient and belongs to *Plantaginetea majoris*, and a *Caricetum canescentis-nigrae*, belonging to *Parvocaricetea* and found in meso- or oligotrophic habitats with an anmoor or peaty fen soil. Within the latter, a

Carex canescens soc. is separable from a *Sphagnum recurvum* subass., on the west coast developed as a *Calamagrostis canescens* variant.

The *marsh vegetation*, *Phragmitetea*, contains *Caricetum acutae* which occurs on wet alluvial soils. This association is split into a *Polygonum amphibium* subass. and a *Campylium polygamum* subass.

The *aquatic vegetation*, *Potametea*, is represented by a *Sparganium minimum* comm. growing in habitats where the water may dry up in summer.

In the chapter *Vegetational changes and soil development* the seral stages in different evolutionary processes have been investigated. The *halo-nitrosere* is divided into two series. The first one comprises a development from *Cakiletum maritimae* via *Atriplicetum littoralis* toward *Agropyro-Rumicion* with increasing stability and decreasing salinity. The second one including perennial drift vegetation is initiated with *Honkenyetum peploidis* and continues via *Honkenyo- Agropyretum acuti* toward *Lepidietum latifolii* and possibly further to *Agropyro-Rosetum rugosae*. The development shows an increasing nitrophilic tendency.

The *xerosere* is split into three subseres. The maritime dune subserie involves a distinct succession from *Elymo-Ammophiletum* via *Violo-Corynephoretum* to *Salici-Empetretum*, and is believed to reach an oak climax forest, *Melampyro-Quercetum roboris*. Also other plant communities may be in climax such as *Pyrolo- Pinetum sylvestris*. Parallel to the vegetational successions there is a progressive soil development from immature soils, viz., dune syrosem, ranker and various transitional types toward podsol. The pH decreases and organic matter increases.

The subserie of the sands affected by man is a succession starting on eroded areas with *Cladonio-Corynephoretum* and continuing via a *Calluna vulgaris* soc. to a climax forest, potentially a *Melampyro-Quercetum roboris* on most localities. The afforestation with pine leads to a semi-stable state, at least in the *Vaccinio- Pinetum sylvestris Empetrum nigrum* subass. The final result is a closing of the plant cover of the earlier open sands. The soil is changed from syrosem or ranker to podsol.

The subserie on inland glaci-fluvial sands comprises a development from *Teesdalia-Corynephoretum* or more rarely *Antherico- Koelerietum glaucae* via *Agrostio-Callunetum* toward *Agrostio- Quercetum roboris*,

probably only subclimax or a richer deciduous forest. An alternative development from *Calluna vulgaris* soc. toward *Melampyro- Quercetum roboris* is less common. The soil evolution is from ranker to mature soils, such as podsoloid which is a transitional type between podsol and brown earth.

The *hygrosere* contains a eutrophic subserie with the seral stages *Caricetum acutae*, *Irido- Alnetum glutinosae* and *Filipendulo- Alnetum glutinosae*, all with oligotrophic contact communities, on various alluvial soils. The oligotrophic subserie contains two separate series. The first one on the west coast comprises a zonation from *Salicetum arenariae Carex nigra* subass. via *Molinio-Myricetum gale* toward *Myrico- Betuletum pubescentis*. The pH seems to decrease and the organic matter increases. The second series illustrated by the condition at Sandhammaren with *Carex rostrata - Juncus effusus* comm. in contact with a mosaic complex of *Caricetum canescentis -nigrae*, *Comaro- Salicetum auritae* and *Polytricho- Betuletum pubescentis* on anmoor or peaty fen soil.

The last chapter deals with the ecological relationships between the maritime sands at Tönnersa (west coast) and Sandhammaren (Baltic coast) with special respect to soil, plant cover and surface water. Of the physical properties the water infiltration was studied by percolation experiments. The variation in horizontal and vertical distribution of various soil parameters such as water content, organic matter, pH and in 0.5 M acetic acid extractable nutrients (Na, K, Ca, Mg, Cl, S, P) in relation to the investigated vegetation units and gradients (*xerosere* and *hygrosere*) is discussed. In the *xerosere* there is an increase of organic matter and nutrients in the surface soil. In the subsoil the humus content decreases, while pH often increases. At Sandhammaren there are much extractable Ca and P in the mineral soil. In the dune depressions Ca is enriched, but P is present in small amounts.

The variation is often combined with the salinity. The Ca/Mg ratios in water from dune depressions are higher at Tönnersa than at Sandhammaren. In the plant cover, investigated for dry weight and mineral nutrients (Na, K, Ca, Mg, Cl, S, P, N), the quotient metals/total elements was higher at Tönnersa than at Sandhammaren, where the Na content in the plant cover was extremely low. N is the dominant element in the vegetation but is present in the soil only in small amounts. The nutrients are in greater storage at Tönnersa than at Sandhammaren.

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Distribution maps



1. *Atriplicetum littoralis*



2. *Cakiletum maritimae*
● *Cakile maritima* soc.



3. *Honkenyetum peplidis*



4. *Honkenyo-Agropyretum acuti*



5. *Lepidietum latifolii*



6. *Elymo-Ammophiletum*
● Typical subass.
● *Hieracium umbellatum* ssp. subass.



7. *Berteroa incana* —
Elymus arenarius community



8. *Cladonia-Corynephorum*
● Typical subass.
● *Cladonia* subass.



9. *Viola-Corynephorum*
● Typical subass.
● *Cladonia* subass.



10. *Teesdalia-Corynephorum*
● Typical subass.
● *Artemisia campestris* subass.



11. *Pleurozium schreberi* —
Agrostis tenuis community



12. *Antherico-Koelerietum glaucae*
● Typical subass.
● *Cladonia* subass.



13. *Festuca ovina* —
Rumex acetosa community



14. *Salicetum arenariae*
● *Ammophila arenaria* subass.
○ *Carex nigra* subass.



15. *Salici—Empetretum*
● *Festuca arenaria* subass.
○ *Polypodium vulgare* subass.
○ *Lophocolea heterophylla* subass.



16. *Calluna vulgaris* soc.



17. *Agrostio—Callunetum*



18. *Agropyro—Rosetum rugosae*



19. *Molinio—Myricetum gale*
Salix arenaria subass.



20. *Molinio—Myricetum gale*
Molinia coerulea soc.



21. *Cladonio—Pinetum sylvestris*
● Typical subass.
○ *Corynephorus canescens* subass.



22. *Vaccinio—Pinetum sylvestris*
● *Empetrum nigrum* subass.
○ *Quercus petraea* subass.



23. *Deschampsia flexuosa* —
Pinus sylvestris community



24. *Agrostis tenuis* — *Populus tremula* community



25. *Oxalis acetosella* —
Quercus petraea community



26. *Melampyro* — *Quercetum roboris*

- Typical subass.
- ① *Corylus avellana* subass.
- ⊖ *Corynephorus canescens* subass.
- ⊗ Inland vicariant



27. *Agrostio* — *Quercetum roboris*



28. *Irido-Alnetum glutinosae*
● *Potentilla palustris* subass.

- ① *Mnium punctatum* subass.



29. *Filipendulo-Alnetum glutinosae*



30. *Myrico-Betuletum pubescentis*



31. *Polytricho* —
Betuletum pubescentis



32. *Carex nigra* —
Calamagrostis epigeios community



33. *Carex rostrata* —
Juncus effusus community



34. *Caricetum canescens-nigrae*
● *Carex canescens* soc.
① *Sphagnum recurvum* subass.



35. *Caricetum acutae*
● *Polygonum amphibium* subass.
① *Campylium polygonum* subass.



36. *Sparganium minimum* community

Tables I-XXII

Table I. *Atriplicetum littoralis* (1); *Cakileetum maritimae* (2-5)

Stand No	1	2	3	4	5
Number of samples	8	12	12	12	10
<i>C-Atriplicetum littoralis</i> et					
<i>Atriplicetum littoralis</i>					
<i>Atriplex littoralis</i>	100 ⁴	8	.	.	10
<i>Tripleurospermum maritimum</i>	62	+	.	.	+
<i>Atriplex calotheca</i>	13	.	.	.	.
<i>C-Cakileetum maritimae</i> et					
<i>Salsola - Honkenyopetum peplidis</i>					
<i>Cakile maritima</i>	.	75 ³	100 ²	100 ⁵	100 ⁴
<i>Atriplex sabulosa</i>	.	8 ³	.	17	.
<i>C-Cakileetum maritimae</i> et					
<i>Cakiletea maritimae</i>					
<i>Salsola kali</i> ssp. <i>kali</i>	25 ³	33 ²	58	8	10
<i>Atriplex latifolia</i>	100 ³	50 ²	.	42	20
Companion taxa					
<i>Agropyron x acutum</i>	62	8	8	17	10
<i>Elymus arenarius</i>	100	+	33	75	50
<i>Honkenya peploides</i>	37	.	8	.	20
<i>Rumex crispus</i>	13	.	.	.	10
<i>Ammophila arenaria</i>	.	+	8	42	.
<i>Ammophila x baltica</i>	13	.	25	.	.
<i>Agropyron repens</i>	50	.	17	.	+
<i>Agrostis stolonifera</i>	13	.	.	.	.
<i>Polygonum lapathifolium</i>	13	.	.	.	.
spp. <i>lapathifolium</i>					

Occasional taxa

Helianthus annuus 1(+), 2(+); *Atriplex* sp. 2(+); *Festuca rubra* 2(+); *Glaux maritima* 2(+); *Scirpus tabernaemontani* 2(+); *Agropyron junceum* ssp. *boreo-atlanticum* 3(+); *Galium aparine* 5(+).

Location of the stands

- 1 *Atriplicetum littoralis*, Fa-1972-6, the spit of Falsterbo, W-side, UB 61303927.
- 2-5 *Cakileetum maritimae*, T8-1966-8 (Stand 2), on the beach bar near the small river Genevadsån, UC 73547275. Sh-1965-9 (Stand 3), on the beach, SW of the lighthouse, VB 46953728.
- 4-5 *Cakile maritima* sociation, Ha-1970-7 (Stand 4), on the beach adjacent to Elymo-Ammophiletum, near the small river Skintan, UC 58338740. Fa-1972-7 (Stand 5), the spit of Falsterbo, W-side, UB 61513930.

Table II. *Honkenyopetum peplidis* (1-4); *Honkenyo - Agropyretum acuti* (5); *Lepidietum latifolii* (6); *Berteroa incana - Elymus arenarius* community (7)

Stand No	1	2	3	4	5	6	7
Number of samples	12	12	12	12	10	8	12
<i>C-dominant Honkenyopetum peplidis</i>							
<i>Honkenya peploides</i>	100	83 ²	100 ⁴	100 ⁵	60	.	.
<i>D-Honkenyopetum peplidis</i>							
<i>Ammophila arenaria</i>	17	8	42	17	.	.	.
<i>Cakile maritima</i>	.	17	67	.	.	.	.
<i>Salsola kali</i> ssp. <i>kali</i>	.	8	58	.	.	.	.
<i>C-Honkenyo-Agropyretum acuti</i> (et							
<i>D-Agropyron x acutum</i> variant)							
<i>Agropyron x acutum</i>	.	.	67	25	100 ²	.	.
<i>C-Lepidietum latifolii</i>							
<i>Lepidietum latifolium</i>	.	.	.	.	.	100 ⁴	.
<i>D-Lepidietum latifolii</i>							
<i>Galium verum</i>	.	.	.	.	.	100	.
<i>G. aparine</i>	.	.	.	.	.	100	.
<i>Bromus hordeaceus</i> ssp. <i>hordeaceus</i>	.	.	.	.	.	50	.
<i>Linaria vulgaris</i>	.	.	.	.	.	50	.
<i>C-Agropyreteia pungentis</i> (vic.							
<i>Honkenyo - Elymetes</i>)							
<i>Elymus arenarius</i>	8	+	42	17	100 ⁵	62 ²	100 ⁵ a)
<i>Rumex crispus</i>	.	.	.	8	10.	25.	.
<i>Solanum dulcamara</i> var. <i>marinum</i>	.	.	.	.	10 ²	37 ²	.
<i>Crambe maritima</i>	.	+	.	.	.	.	.
Lokal C-Berteroa incana - Elymus							
<i>arenarius</i> comm.							
<i>Berteroa incana</i>	.	.	.	.	.	.	50
Lokal D-Berteroa incana - Elymus							
<i>arenarius</i> comm.							
<i>Polygonum amphibium</i>	.	.	.	.	.	.	92
<i>Brachythecium rutabulum</i>	.	.	.	.	.	.	50
<i>Polygonum convolvulus</i>	.	.	.	.	.	.	42
Companion taxa							
<i>Atriplex littoralis</i>	.	.	25	.	+	.	.
<i>A. latifolia</i>	.	.	17	.	+	.	.
<i>Tripleurospermum maritimum</i>	.	.	.	.	10	13	.
<i>Agropyron repens</i>	.	.	25	33	30	100 ²	83
<i>Festuca rubra</i>	.	.	.	.	.	.	83
<i>Ammophila x baltica</i>	.	.	.	.	30	.	.
<i>Festuca arenaria</i>	.	.	.	.	.	37	.
<i>Achillea millefolium</i>	.	.	.	.	.	.	25
<i>Agrostis tenuis</i>	.	.	.	.	.	.	17
<i>Viola tricolor</i>	.	.	.	.	.	.	17
<i>Urtica dioica</i>	.	.	.	.	.	.	17

a) *Elymus arenarius* is a dominant companion taxon of *Berteroa incana* - *Elymus arenarius* comm.

Occasional taxa

Artemisia vulgaris 6(13); *Carex arenaria* 6(13); *Alopecurus pratensis* 7(8); *Atriplex sabulosa* 3(+); *A. sp.* 3(+); *Festuca arundinacea* 5(+); *Lathyrus maritimus* 5(+); *Cirsium arvense* 6(+); *Poa pratensis* 6(+); *Anchusa officinalis* 7(+); *Galeopsis tetrahit* 7(+); *Centaurea scabiosa* 7(+); *Urtica urens* 7(+).

Location of the stands

- 1-4 *Honkenyopetum peplidis*, T8-1966-5 (Stand 1), on the beach bar, near the river Genevadsån, UC 73527295. T8-1966-8 (Stand 2), on the beach bar, near the river Genevadsån, UC 73547270.
- 3-4 *Agropyron x acutum* variant, Kh-1965-8 (Stand 3), on the beach, just in front of the low dunes, UC 63953402. Kh-1970-6 (Stand 4), on the beach bar, just in front of the low dunes, UC 63203350.
- 5 *Honkenyo-Agropyretum x acuti*, Fa-1972-6, the spit of Falsterbo, W-side, UB 61363934.
- 6 *Lepidietum latifolii*, Fa-1972-7, the spit of Falsterbo, W-side, rather stable sand, UB 61373937.
- 7 *Berteroa incana* - *Elymus arenarius* community, Silvåkra 1967-7, military training area, near the small river Klingavälsån, VB 07707365.

Table III. Elymo-Amphiletum (1-31)

[illegible]

San, UC 73557250. TP-1965-7 (Stand 8), on the low seaward dunes, N parts, UC 73557260. SH-1966-8 (Stand 9), on the low dunes, SN 47053735. SH-1965-9 (Stand 10), on the low seaward dunes, SN of the lighthouse, VB 47837729. VH-1965-9 (Stand 11), on the low seaward dunes, VB 50017402. TP-1965-9 (Stand 12) on the low seaward dunes, VB 51258775. TP-1966-9 (Stand 13), on the low seaward dunes, S parts, UC 73807020. SH-1965-8 (Stand 14), on the low seaward dunes, SN of the lighthouse, VB 47703745.

Ammophila arenaria ssp. *prostrata* (Stand 15), on the low seaward dunes, S parts, UC 73727020. TÖ-1966-5 (Stand 16), on the low seaward dunes, S parts. UC 73737017.

Hieracium umbellatum ssp. subass., Ha-1965-7 (Stand 17), on the seaward dunes, S of the small river Skintan, U. 58318705; Ha-1965-7 (Stand 18), on the seaward dunes, E of the small river Skintan, U. 58318695. Ha-1965-7 (Stand 19), on the seaward dunes, S parts, U. 7317080; Ha-1965-7 (Stand 20), on the seaward dunes, N parts, U. 7317079; Ha-1965-7 (Stand 21), on the seaward dunes, S parts, U. 7317078; Ha-1965-7 (Stand 22), on the seaward dunes, S parts, U. 7317077; Ha-1965-7 (Stand 23), on the seaward dunes, SW of the lighthouse, U. 731670375; Ha-1965-7 (Stand 24), on the seaward dunes, SW of the lighthouse, U. 731670375; Ha-1965-7 (Stand 25), on the seaward dunes, SW of the lighthouse, U. 731670375; Ha-1965-7 (Stand 26), on the seaward dunes, SW of the lighthouse, U. 48174735; Ha-1965-7 (Stand 27), on the seaward dunes, N parts, U. 736571270; Ha-1965-7 (Stand 28), on the seaward dunes, N parts, U. 736571270; Ha-1965-7 (Stand 29), on the seaward dunes, VB 51288775; Ha-1965-7 (Stand 30), on the seaward dunes, VB 51288775.

Agropyron repens variant, Xh-1965-8, on the low seaward dunes, IUC 63953403.

1-16 *Elymo-Ammophiletum* (typical subass.), Ha-1970-7 (Stand 6), on the low seaward dunes, S of the small river near the river Conander.

SKINTAN, U. 38308/30, 10-1966-8 (Stand 1), on the low seaward dunes of the beach bar, near the river levee.

Table IV. *Cladonio(districtae)-Corynephorum* (1-12)

Stand No	1	2	3	4	5	6	7	8	9	10	11	12
Number of samples	10	12	12	12	12	12	12	12	12	8	10	12
<u>C-Cladonio-Corynephorum, Spargulo-</u>												
<u>Corynephorion et Corynephoretalia</u>												
<i>Cladonia dstricta</i>	.	.	.	.	+	.	.	.	.	.	100 ⁴	.
<i>Stereocaulon condensatum</i>	.	.	.	.	.	.	.	.	.	.	70	.
<u>D-Cladonia subass.</u>												
<i>Cladonia arbuscula et mitis</i>	20	92	83	100	92	92 ²	100	100 ⁴	100 ⁴	100 ⁴	80	100
<i>C. chlorophaea coll.</i>	.	83	100	100	83	83 ²	33	50 ²	58	75	80	100
<i>C. impexa</i>	.	42 ²	25	83 ²	92 ³	100 ²	50	100 ²	42	37	+	33
<i>C. cornuta et gracilis</i>	.	50 ²	17	67 ²	50 ³	50	33	58	42	62	100	83
<i>C. floerkeana</i>	.	58	33	33	42	33	8	.	83	50	.	25
<i>C. pleurota</i>	.	33	50	.	17	42	58	.	.	13	40	50 ³
<i>C. uncialis</i>	.	33	.	100	25	25	25	83	.	.	10	92 ³
<u>D-Cetraria crispa variant</u>												
<i>Cetraria crispa</i>	10	.	.	.	.	.	33	50	17	13	.	50
<i>C. islandica</i>	.	.	.	.	.	.	.	67	.	75	40	42
<u>C-Koelerio-Corynephoretea</u>												
<i>Corynephorus canescens</i>	100 ³	100 ²	100 ²	100 ³	100 ²	100 ³	100	42 ²	100	62 ²	60	42 ²
<i>Carex arenaria</i>	40	75	75	75 ³	75 ³	100	100 ³	100 ²	100	100 ²	60	100 ⁵
<i>Cornicularia aculeata</i>	60	100	83	100 ³	100 ³	92	100 ³	100 ²	100	100	100	100 ⁵
<i>Festuca poeasica</i>	70	25	75	25	+	33	.	.	42	.	20	.
<i>Ceratodon purpureus</i>	.	.	42	.	17	42	17	8	50	.	.	.
<i>Cladonia alciornis</i>	.	.	.	8	.	.	33	17	.	.	.	17
<i>Polytrichum piliferum</i>	.	.	.	.	.	.	92	17	.	.	30	100
<i>Koeleria glauca</i>	.	50	8	25	+	.	.	.	.	.	.	.
<i>Festuca arenaria</i>	40	.	.	.	.	.	.	.	.	.	.	.
<i>Viola canina var. dunensis</i>	.	.	.	.	.	.	17	.	17	.	.	.
<i>Cladonia furcata</i>	.	25	+	.	.	.	.	.	8	.	.	8
<i>Viola tricolor ssp. curtisii</i>	.	.	.	.	.	.	33	.	.	.	.	8
<i>Rhacomitrium canescens</i>	.	.	.	.	.	.	.	.	+	.	30	.
<i>Jasione montana var. littoralis</i>	.	.	17	.	.	.	8	.	.	.	.	+
<i>Hieracium umbellatum</i> ssp.	.	8	17	.	.	.	.	.	.	.	.	+
<i>Rumex tenuifolius</i>	.	.	.	.	.	.	.	.	.	.	.	+
<u>Companion taxa</u>												
<i>Ammophila arenaria</i>	20	58	83	8	33	92 ²	67	.	8	.	.	75
<i>Dicranum scoparium</i>	.	50	+	50	.	58 ²	.	17	.	13	.	8
<i>Parmelia physodes</i>	.	58	58	8	25	25	.	.	17	.	.	8
<i>Cladonia cenomyce</i> indet.	.	17	17	42	58	.	.	8	33	13	.	17
<i>C. cornutoradiata</i>	.	.	83	.	8	8	50	.	8	.	.	42
<i>Cephalozia</i> sp.	.	.	25 ²	25	25	33	17	.	50	.	.	.
<i>Agrostis tenuis</i>	.	50	.	.	.	.	42	.	.	.	.	.
<i>Pycnothelia papillaria</i>	.	.	.	.	.	.	.	.	.	.	40	.

Occasional taxa
Calluna vulgaris 3(8), 5(17), 7(+), 12(+); *Cladonia rangiferina* 5(17), 6(8); *C. fimbriata* 4(25); *Salix arenaria* 2(+), 5(8), 12(+); *Ammophila x baltica* 2(8), 3(+); *Galium verum* 2(8), 5(+); *Cetraria glauca* 3(8); *Pohlia nutans* 3(8); *Empetrum nigrum* 2(+), 3(+), 7(+), 12(+); *Pinus sylvestris* juv. 2(+), 6(+), 12(+); *Hieracium pilosella* 7(+); *Pinus mugo* juv. 7(+); *Ptilidium ciliare* 6(8); *Cladonia crispata* 11(+); *Stereocaulon* sp. 11(+).

Location of the stands
1 Typical subass. (= *Corynephorus canescens* soc.), Fb-1970-10, sandy plain inland from the seaward dunes, VB 51048790.
2-12 *Cladonia subass.*, Sh-1965-8 (Stand 2), inland from the seaward dunes, VB 47803765. Sh-1965-8. (Stand 3),

hollow inland from the seaward dunes, VB 46853737. Sh-1967-11 (Stand 4), inland from the seaward dunes, VB 47903764. Sh-1966-9 (Stand 5), inland from the seaward dunes, VB 78453788. Sh-1966-9 (Stand 6), inland from the seaward dunes, VB 48603796.
7-12 *Cetraria crispa* variant, Ah-1965-8 (Stand 7), inland from the seaward dunes, UC 64053380. Ah-1970-6 (Stand 8), inland from the seaward dunes, UC 63903365. Fb-1965-9 (Stand 9), sandy plain, inland from the seaward dunes, VB 51108775. Fb-1970-7 (Stand 10), sandy plain, inland from the seaward dunes, VB 51108785. Fb-1970-10 (Stand 11), sandy plain, inland from the seaward dunes, VB 50958790. Ah-1965-8 (Stand 12), inland from the seaward dunes, adjacent to *Salici-Empetretum* and *Vaccinio-Pinetum sylvestris*, UC 64153385.

Table V. *Violo-Corynephorum* (1-13)

Stand No	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of samples	12	12	11	10	12	10	12	12	11	12	12	12	12
C-Violo-Corynephorum													
<i>Viola canina</i> var. <i>dunensis</i>	42	33 ²	45	80	8	40	17	+	27	+	8	.	8
<i>D-Cladonia subass.</i>	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cladonia arbuscula</i> et <i>mitis</i>	.	8	8	.	33	.	100 ⁴	67 ²	82	92	67	67 ²	33
<i>Dicranum scoparium</i>	.	.	.	.	.	.	67	25	44	58	25	33 ²	25
<i>Cladonia cornuta</i> et <i>gracilis</i>	.	17	.	.	.	.	17	83	64 ⁴	100 ³	58	100 ²	92
<i>C. impezia</i>	.	.	.	.	.	.	.	58	100 ⁴	100 ³	33	100	17
<i>C. floerkeana</i>	.	.	.	.	8	.	.	58	36	.	75	83	67
<i>C. pleurota</i>	.	.	.	.	.	.	.	33	9	.	58	75	50
C-Galio-Koelerion													
<i>Hieracium umbellatum</i> ssp.	8	8	64	100 ²	75	60	92	17	+	+	75	92	75
<i>Jasione montana</i> var. <i>littoralis</i>	8	25 ²	36	20	25	+	100	.	.	.	33	67	42
<i>Festuca arenaria</i>	75	100 ²	64	100	25	90	.	.	.	17	42	.	.
<i>Viola tricolor</i> ssp. <i>curtisii</i>	42	42	36	20	.	.	.	.	.	.	17	8	8
C-Festuco-Sedetalia et Koelerio-Corynephoretea													
<i>Corynephorus canescens</i>	100 ²	92	100 ³	90 ²	75 ³	60	100 ²	100	100 ²	100 ²	100 ²	92	100 ²
<i>Carex arenaria</i>	83 ²	8 ²	18 ²	90	100 ³	90	92	100	82 ²	83	83	100	17
<i>Cornicularia aculeata</i>	+	100 ²	73 ²	+	25	100	100	100	91 ²	58	83	75	58 ²
<i>Ceratodon purpureus</i>	8	42	64	.	100 ²	10	33	17	.	25	50	.	25 ²
<i>Cladonia furcata</i>	.	17	.	.	75	80	33	8	8 ²	75	33	33 ²	.
<i>Polytrichum piliferum</i>	33	75	45	.	.	.	.	83	91 ²	67 ²	8	.	25 ²
<i>Festuca polesica</i>	.	.	.	100 ²	100	100 ²	92	.	.	.	58	67	+
<i>Cladonia alpicornis</i>	.	8	.	.	.	.	8	75	36	8	.	17	.
<i>Koeleria glauca</i>	.	.	.	.	.	30	25	.	.	.	83	83	33
<i>Helichrysum arenarium</i> (D-variant)	.	.	.	.	8	70 ²	50	.	.	.	.	.	.
<i>Thymus serpyllum</i> (D-variant)	.	.	.	.	.	100 ²	92	.	.	.	.	.	.
<i>Dianthus arenarius</i> (D-variant)	.	.	.	.	.	30	100	.	.	.	.	.	.
<i>Rhacomitrium canescens</i> (D-variant)	.	.	.	.	.	70	42	.	.	8	.	.	.
<i>Brachythecium albicans</i>	.	.	.	.	67	30	+	.	.	.	.	.	.
<i>Rumex tenuifolius</i>	.	.	.	10	.	.	.	.	.	.	25	.	.
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	.	.	.	.	.	.	92	.	.	.	.	.	.
<i>Trifolium campestre</i>	.	.	.	.	.	.	8	.	.	.	.	.	.
<i>Tortula ruralis</i> var. <i>ruraliformis</i>	.	.	.	.	+	.	.	.	.	.	.	.	.
<i>Teesdalia nudicaulis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion taxa													
<i>Amphiphila arenaria</i>	25	42	45	50	8	10	17	100	73	75	100	100	75
<i>Amphiphila x baltica</i>	.	.	.	.	8	10	.	.	.	.	50	25	92
<i>Artemisia campestris</i>	.	100 ²	55	50	.	100	58	.	.	.	+	.	.
<i>Galium verum</i>	.	.	.	100	75	100	92	.	.	.	17	75	.
<i>Empetrum nigrum</i>	25	+	+	.	.	.	.	8	27	+	+	8	.
<i>Luzula campestris</i>	.	.	.	30	.	.	25	25	.	+	.	.	.
<i>Cladonia chlorophaea</i> coll.	.	33	27	.	67	.	67	75	64	.	67	100	100
<i>Cephalozicella</i> sp.	.	.	.	.	25	.	58	33	18	.	75	75	33
<i>Cladonia fimbriata</i>	.	8	.	.	100	.	17	.	.	.	83	25	17
<i>C. cenomyce</i> indet.	.	25	36	.	8	.	42	27	33	.	33	.	.
<i>C. cornutoradiata</i>	.	.	.	.	25	.	8	.	.	.	50	50	33
<i>Hypochoeris radicata</i>	.	.	.	20	.	.	58	.	.	.	17	8	.
<i>Parmelia physodes</i>	.	25	36	.	17	.	17	.	.	.	8	42	17
<i>Pohlia nutans</i>	.	17	.	.	8	.	.	.	.	.	42	8	33
<i>Cetraria islandica</i>	.	.	.	.	.	50	8	.	.	.	17	.	.
<i>Cladonia uncialis</i>	.	.	.	.	.	.	33	36	.	.	8	.	.
<i>C. rangiferina</i>	.	.	.	.	.	.	17	36	.	.	.	.	.
<i>Hieracium pilosella</i>	.	.	.	.	.	.	67	.	.	.	.	.	.

Occasional taxa

Pycnotheria papillaria 8(8), 10(8), 13(8); *Elymus arenarius* 2(+), 5(17), 6(20); *Agrostis tenuis* 3(+), 4(20), 7(8); *Polypodium vulgare* 12(8), 13(+); *Polytrichum juniperinum* 13(25); *Carex hirta* 7(17); *Anemone pratensis* 6(10); *Cetraria glauca* 13(8); *Usnea hirta* 13(8); *Dactylis glomerata* 11(8); *Salix arenaria* 12(8); *Pimpinella saxifraga* 7(8); *Honkenya pepioides* 3(+); *Taraxacum* sp. 6(+); *Quercus robur* juv. 12(+); *Calluna vulgaris* 13(+).

Location of the stands

1-13 *Violo-Corynephorum* (1-6 = typical subass.), Tö-1966-9 (Stand 1), on the seaward dunes, N parts, UC 73657250. Tö-1967-7 (Stand 2), on the seaward dunes, N parts, UC 73577285. Tö-1965-7 (Stand 3), on the seaward dunes, N parts UC 73577285. Fa-1972-7 (Stand

4), on the low seaward dunes, S side of the spit of Falsterbo, UB 61803940. Fö-1965-9 (Stand 5), on the sandy plain, behind the seaward dunes, VB 51058780.

6-7 *Dianthus arenarius* variant, Vm-1971-9 (Stand 6), on the very low seaward dunes, VB 50027380. Vm-1965-9 (Stand 7), on the very low seaward dunes, VB 49977405.

7-13 *Cladonia subass.*, Tö-1965-7 (Stand 8), on the seaward dunes, S parts, UC 73757075, Tö-1965-7 (Stand 9), on the seaward dunes, S parts, UC 73747077. Tö-1967-10 (Stand 10), on the seaward dunes, S parts, UC 73807045. Sh-1965-8 (Stand 11), on the seaward dunes, SW of the lighthouse, VB 48503775. Sh-1965-9 (Stand 12), on the seaward dunes, SW of the lighthouse, VB 47703752. Sh-1965-8 (Stand 13), on the seaward dunes, SW of the lighthouse, VB 48523776.

Table VI. *Teesdalia-Corynephorum* (1-13); *Festuca ovina-Rumex acetosa* community (14)

Stand No	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of samples	8	12	12	12	10	12	12	12	10	12	12	10	10	12
C-Teesdalia-Corynephorum et Thero-Airion														
<i>Agrostis canina</i> ssp. <i>montana</i>	75	100	67	100 ²	10	83	58 ²	.	.	100 ²	100 ²	100	.	.
<i>Teesdalia nudicaulis</i>	37	8	.	42	90	.	75	58	10	67	+	.	.	.
<i>Aira praecox</i>	.	.	.	.	.	.	.	.	40	.	.	10	10	.
<i>Filago minima</i>	.	.	+	.	.	.	75	.	.	.	.	.	.	.
D-Teesdalia-Corynephorum														
<i>Cladonia glauca</i>	.	.	.	58	90	25	.	75	10	8	100 ²	.	50	.
<i>C. degenerans</i>	.	.	.	100 ²	80	8	.	92	.	8	58	.	.	.
<i>C. verticillata</i>	.	.	.	50	50	42	.	67	.	.	.	.	.	.
D-Artemisia campestris subass.														
<i>Artemisia campestris</i>	.	.	.	+	.	.	33	58	90	100	58	80	100 ³	50
<i>Hypnum cupressiforme</i> coll.	.	.	.	.	.	.	50	8	20	67	17	10	40	8
<i>Achillea millefolium</i>	.	.	.	.	.	.	67	8	80	8	.	90	70	75
<i>Luzula campestris</i>	.	.	.	.	.	.	.	42	.	.	.	30	10	83

Table VI. Continued

Stand No	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of samples	8	12	12	12	10	12	12	12	10	12	12	10	10	12
D-variants														
<i>Senecio vernalis</i>	50	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cerastium semidecandrum</i>	50	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Galium verum</i>	.	.	.	.	.	.	.	.	.	.	58	10	.	17
<i>Euphorbia cyparissias</i>	.	.	.	.	.	.	.	.	.	.	58	.	.	.
<i>Oenothera biennis</i>	.	.	.	.	.	.	.	.	.	.	.	50	.	.
<i>Anthyllis vulneraria</i>	.	.	.	.	.	.	.	.	.	.	.	40	.	.
<i>Arenaria serpyllifolia</i>	.	.	.	.	.	.	.	.	.	.	.	.	50	.
<i>Asparagus officinalis</i>	.	.	.	.	.	.	.	.	.	.	.	.	30	.
<i>Convolvulus arvensis</i>	.	.	.	.	.	.	.	.	.	.	.	.	30	.
C-Festuco-Sedetalia et Koelerio-Corynephoretea														
<i>Corynephorus canescens</i>	100 ³	100 ³	100 ²	100 ³	100 ⁴	58	100 ³	100 ³	100 ³	42	+	100 ²	80	.
<i>Polytrichum piliferum</i>	.	100 ⁴	100 ⁴	100 ³	70 ³	100 ⁵	100	67	90	33	17	100	30	.
<i>Rumex tenuifolius</i>	.	.	50	75	100	33	92	92	100	92	100	40	70	.
<i>Scleranthus perennis</i>	.	.	17	8	40	42	67	58	.	67	67	100 ²	10	42
<i>Jasione montana</i>	.	.	67	.	.	92	92	42	100 ³	92	100	100 ²	100	8
<i>Cladonia furcata</i>	.	.	.	17	.	42	58	100 ²	90 ³	+	25	10 ³	100 ²	42
<i>Ceratodon purpureus</i>	.	.	100	.	.	8	83	75	90	.	.	100 ³	90 ²	.
<i>Helichrysum arenarium</i>	.	.	.	.	.	.	.	8	100	33	42	50	100	8
<i>Carex arenaria</i>	50	100	.	.	.	92	.	.	.	100 ²	100 ²	10	.	.
<i>Thymus serpyllum</i>	.	8	.	.	.	.	+	.	.	100 ²	17	.	.	67
<i>Brachythecium albicans</i>	.	.	.	.	.	.	17	+	30	8	.	10	90	.
<i>Rhacomitrium canescens</i>	.	100 ⁴	.	.	.	58	+	25 ²	.	8	.	30 ³	.	.
<i>Trifolium arvense</i>	.	.	.	.	.	.	8	.	30	8	.	100 ³	90	.
<i>Cornicularia aculeata</i>	.	100	.	33	.	.	.	.	.	42	25	.	.	.
<i>Cladonia rangiferinis</i>	.	.	.	.	.	.	.	.	30	+	17	.	20	.
<i>Hypericum perforatum</i>	.	.	.	.	.	.	.	.	.	+	.	10	.	50
<i>Dianthus deltoides</i>	.	.	.	.	.	.	.	.	.	8	.	.	.	.
<i>Campanula rotundifolia</i>	.	.	.	.	.	.	.	.	.	.	17	.	.	+
<i>Trifolium campestre</i>	.	.	.	.	.	.	.	.	.	.	.	70	.	.
<i>Ononis repens</i>	.	.	.	.	.	.	.	.	.	.	.	40 ²	.	.
<i>Herniaria glabra</i>	.	.	.	.	.	.	.	.	.	.	.	20	.	.
<i>Potentilla argentea</i>	.	.	.	.	.	.	.	.	.	.	.	20	.	.
<i>Vicia lathyroides</i>	.	.	.	.	.	.	.	.	.	.	.	.	10	.
<i>Armeria maritima</i> var. <i>elongata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Local C-Festuca ovina-Rumex acetosa community														
<i>Rumex acetosa</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	42
<i>Holcus lanatus</i>	.	.	.	.	.	.	8	.	.	.	.	.	.	42
<i>Plantago lanceolata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	25
D-Festuca ovina-Rumex acetosa community														
<i>Festuca ovina</i>	.	17	.	.	.	.	.	17	.	.	.	10	.	100 ⁴
<i>Pleurozium schreberi</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	100 ³
<i>Anthoxanthum odoratum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	75
<i>Hylocomium splendens</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	33
<i>Stellaria graminea</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	25
C-Molinio-Arrhenatheretea														
<i>Knaulia arvensis</i>	.	.	.	.	.	.	.	8	.	.	+	.	.	42
<i>Arrhenatherum elatius</i>	.	.	.	.	.	.	.	.	.	.	.	.	40	25
<i>Veronica chamaedrys</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	42
<i>Rhytidadelphus squarrosus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	17
Companion taxa														
<i>Cladonia arbuscula</i> et <i>mitis</i>	.	83	.	83	100 ²	58	8	83	30	8	75	.	20	.
<i>C. cornuta</i> et <i>gracilis</i>	.	.	.	33	100 ²	58	.	33	60	8	100	.	10	.
<i>C. implexa</i>	.	.	.	33	20	.	.	.	30	.	42	.	10	.
<i>Cetraria islandica</i>	.	50	.	.	.	.	.	.	.	.	.	.	.	.
<i>Pinus sylvestris</i> juv.	.	.	8	.	.	.	.	33	.	.	.	.	.	33
<i>Agrostis tenuis</i>	.	25	100 ³	8	.	100	83	75	40	67	83	100 ²	20	92
<i>Cladonia chlorophaea</i> coll.	.	25	17	42	60	50	83	25	90 ²	100	58	.	50	.
<i>Hieracium pilosella</i>	.	.	8	+	.	50	100	92 ²	100 ³	67	75	20	100 ⁴	100 ³
<i>Hypochoeris radicata</i>	.	+	17	.	10	75	+	.	.	25	17	10	.	17
<i>Hieracium umbellatum</i>	.	25	67	17	.	83	.	25	.	42	100	40	.	+
<i>Cephalozia</i> sp.	.	.	33	67	70	42	17	25	.	33	42	.	.	.
<i>Polytrichum juniperinum</i>	.	.	25	17	80	17	25	.	.	8	.	20	10	17
<i>Cladonia pleurota</i>	.	.	.	.	100	80	17	.	17	10	17	67	.	.
<i>C. floerkeana</i>	.	.	.	58	80	50	.	100	20	.	25	.	.	.
<i>Festuca rubra</i>	.	.	58	.	.	.	67	.	.	8	.	30	.	75
<i>Cladonia cornutoradiata</i>	.	.	100	.	10	92	100	.	.	.	.	.	.	8
<i>C. fimbriata</i>	.	.	83	.	10	.	.	.	.	.	.	10	.	17
<i>Viola canina</i>	13	.	.	.	.	.	.	.	.	42	+	.	.	.
<i>Dicranum scoparium</i>	.	.	.	.	30	.	.	.	.	8	42	.	.	.
<i>Pohlia nutans</i>	.	.	.	.	80	.	.	.	.	.	.	.	.	.
<i>Brachythecium rutabulum</i>	.	.	.	.	.	.	.	.	.	.	.	.	10	67
<i>Lophocolea bidentata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	33

Occasional taxa

Peltigera canina coll. 8(+), 9(10), 10(8), 11(8), 13(20), 14(+); *Cladonia cenomyce* indet. 7(17), 9(10), 12(20), 13(30); *Parmelia physodes* 6(8), 8(8), 11(8); *Scleropodium purum* 9(10), 12(10), 13(20); *Cerastium arvense* 9(10), 10(8), 13(10); *Erigeron acre* ssp. *acre* 9(10), 10(+), 13(10); *Cladonia rangiferina* 5(10), 6(8); *Quercus robur* juv. 8(8), 14(25); *Viola tricolor* 7(8), 10(+); *Veronica officinalis* 13(10), 14(8); *Bryum* sp. 5(30); *Cladonia crispata* 14(25); *Cladonia elongata* 14(25); *Spergula arvensis* 5(20); *Calluna vulgaris* 2(+), 5(10), 9(+), 10(+), 14(17); *Ptilium crista-castrensis* 14(17); *Cetraria crispa* 2(17); *Erigeron canadense* 12(10); *Holcus mollis* 12(10); *Mnium affine* 12(10); *Poa pratensis* 12(10); *Cladonia pityrea* 6(8); *Cerastium vulgatum* 14(8); *Anchusa officinalis* 4(+); *Centaurea scabiosa* 11(+).

Location of the stands

- 1-6 *Teesdalia-Corynephoretum* typical subass., Flyinge-1972-6 (Stand 1 = *Senecio vernalis* variant), a sand pit on a small hill, UB 98057940.
2-6 *Polytrichum piliferum* dominant variant, Revingehed-1967-8 (Stand 2), a sandy hill, VB 05027575. Vitaby-1965-9 (Stand 3), between the church and Vitemölla, glaci-fluvial sand, VB 48707310. Vomb-1967-7 (Stand 4), between the

church and Klingavälsån, glaci-fluvial sand, VB 08307190. Hemmestorp-1970-10 (Stand 5), glaci-fluvial sand, just near a sand pit, VB 09606513. Vitaby-1965-9 (Stand 6), between the church and Vitemölla, glaci-fluvial sand, VB 48717312.

- 7-13 *Artemisia campestris* subass., Silvåkra-1967-7 (Stand 7), military training area, near Klingavälsån, VB 07757335. Björka (Stand 8), on a small sandy hill, near the small river Björkaån, VB 15506840. Alstorp (Stand 9), glaci-fluvial sand, near a sand pit, UB 73448685. Silvåkra-1967-7 (Stand 10), military training area, near Klingavälsån, VB 07657382.
11 *Euphorbia cyparissias* variant, Vomb-1967-8, between the church and Klingavälsån, glaci-fluvial sand, VB 08287188.
12 *Oenothera biennis* variant, Alstorp-1971-8, glaci-fluvial sand, an abandoned sand pit, UB 73478660.
13 *Asparagus officinalis* variant, Alstorp-1971-8, glaci-fluvial sand, near the main road, UB 73508684.
14 *Festuca ovina-Rumex acetosa* community, Björka-1967-7, a small sandy hill, near the small river Björkaån, VB 15456843.

Table VII. *Antherico-Koelerietum glaucae* (1-2);*Pleurozium schreberi*-*Agrostis tenuis* community (3-4)

Stand No	1	2	3	4
Number of samples	8	12	12	12
<i>C-Antherico-Koelerietum glaucae</i> et <i>Koelerion glaucae</i>				
<i>Koeleria glauca</i>	100 ²	100	.	.
<i>Festuca poeisia</i>	100	100	.	.
<i>Dianthus arenarius</i>	13	83	.	.
<i>Astragalus arenarius</i>	13	50	.	.
<i>Androsace septentrionalis</i>	+	+	.	.
<i>D-Cladonia</i> subass.				
<i>Cladonia arbuscula</i> et <i>mitis</i>	100 ²	100 ³	+	25
<i>C. chlorophaea</i> coll.	87	100	75	.
<i>D-Anthericum liliago</i> variant				
<i>Anthericum liliago</i>	100 ²	.	.	.
<i>Cerastium semidecandrum</i> coll.	75	.	.	.
Local <i>D-combination Pleurozium schreberi</i>				
<i>Agrostis tenuis</i> community				
<i>Pleurozium schreberi</i>	.	.	83 ⁴	100 ⁴
<i>Agrostis tenuis</i>	.	.	100	33
<i>D-Deschampsia flexuosa</i> variant				
<i>Ammophila arenaria</i>	.	.	100 ²	8
<i>Deschampsia flexuosa</i>	.	.	92 ³	8
<i>C-Festuco-Sedetalia</i> et <i>Koelerio-Corynephoretea</i>				
<i>Carex arenaria</i> (D-variant)	50	42	.	100 ⁴
<i>Cornicularia aculeata</i>	75	100 ²	25	.
<i>Cladonia furcata</i>	100 ²	25	42	42
<i>Corynephorus canescens</i>	75	100	17	.
<i>Ceratodon purpureus</i>	13	92	42	.
<i>Thymus serpyllum</i>	100	92	.	.
<i>Rhacomitrium canescens</i>	100 ²	33	.	.
<i>Sedum acre</i>	75	50	.	.
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	25	75	.	.
<i>Helichrysum arenarium</i>	25	42	.	.
<i>Hieracium umbellatum</i> ssp.	25	17	.	.
<i>Festuca arenaria</i>	.	.	17	8
<i>Viola tricolor</i> ssp. <i>curtisii</i>	.	.	92	.
<i>Cladonia pitryea</i>	.	58	.	.
<i>C. alcicornis</i> var.	13	25	.	.
<i>Viola rupestris</i>	.	17	.	.
<i>Jasione montana</i> var. <i>littoralis</i>	.	17	.	.
<i>Phleum arenarium</i>	13	.	.	.
<i>Aira praecox</i>	.	.	8	.
<i>Polytrichum piliferum</i>	.	.	8	.
<i>Anthyllis vulneraria</i> ssp. <i>maritima</i>	.	+	.	.
<i>Tortula ruralis</i> var. <i>ruraliformis</i>	.	+	.	.
Companion taxa				
<i>Galium verum</i>	100	83	.	33
<i>Anemone pratensis</i>	25	83	.	.
<i>Artemisia campestris</i>	13	25	.	.
<i>Pimpinella saxifraga</i>	.	33	.	.
<i>Dicranum scoparium</i>	.	8	42 ²	17
<i>Cephalozia</i> sp.	.	67	67	.
<i>Cladonia fimbriata</i>	.	42	42	.
<i>C. cornutoradiata</i>	.	17	50	.
<i>Polypodium vulgare</i>	.	.	33	+
<i>Parmelia physodes</i>	.	.	67	.
<i>Polytrichum juniperinum</i>	.	.	58	.

Occasional taxa
Brachythecium rutabulum 3(17), 4(17); *Pinus sylvestris* juv. 2(13), 3(8); *Cladonia impexa* 2(8), 3(8); *C. cornuta et gracilis* 2(+), 3(8); *Medicago lupulina* 1(13); *Cetraria crispa* 2(17); *C. islandica* 2(17); *Hieracium pilosella* 2(8); *Cladonia cenomyce* indet. 3(25); *Dicranum undulatum* 3(25); *Lophocolea bidentata* 3(25); *Pohlia nutans* 3(25); *Hypnum cupressiforme* coll. 3(8); *Achillea millefolium* 4(17); *Viola canina* var. *denensis* 4(17); *Chamaenerion angustifolium* 4(25); *Agropyron repens* 4(8); *Sedum telephium* 4(8); *Dryopteris spinulosa* 3(+); *Elymus arenarius* 3(+); *Pinus mugo* juv. 3(+).

Location of the stands

1-2 *Antherico-Koelerietum glaucae*, Vm-1972-6 (Stand 1 = *Anthericum liliago* variant), on the top of the steep slope, near planted pines, VB 49807390, Vm-1965-9 (Stand 2), on the middle of the steep slope, below the planted pines, VB 49857450.

3-4 *Pleurozium schreberi*-*Agrostis tenuis* community, Xh-1965-8 (Stand 3 = *Deschampsia flexuosa* variant), on the low seaward dunes, UC 64043406.

4 *Carex arenaria* variant, Xh-1970-6, on the low seaward dunes, UC 63703375.

Table VIII. *Salicetum arenariae* (1-5); *Agropyro - Rosetum rugosae* (6)

Stand No	1	2	3	4	5	6
Number of samples	12	8	11	12	12	12
<i>C-dominant Salicetum arenariae</i>						
<i>Salix arenaria</i>	100 ⁵	100 ⁴	91 ⁵	100 ⁵	100 ⁴	.
<i>D-Ammophila arenaria</i> subass.						
<i>Ammophila arenaria</i>	42	62	65	.	.	.
<i>Festuca arenaria</i>	33	87	18	.	.	17
<i>D-Carex nigra</i> subass.						
<i>Carex acuta</i>	.	.	.	67	100	.
<i>C. nigra</i>	.	.	.	58	33	.
<i>Galium uliginosum</i>	.	.	.	17	33	.
<i>Veronica scutellata</i>	.	.	.	17	8	.
<i>D-Corynephorus canescens</i> variant						
<i>Corynephorus canescens</i>	.	100	64	.	.	.
<i>Jasione montana</i>	.	87	44	.	.	.
<i>Elymus arenarius</i>	.	25	91	.	.	.
<i>Parmelia physodes</i>	.	37	82	.	.	.
<i>Viola tricolor</i> ssp. <i>curtisii</i>	.	+	44	.	.	.
<i>C-Nardo-Callunetea</i>						
<i>Calluna vulgaris</i>	.	.	9	17	8	.
<i>Luzula multiflora</i>	.	.	.	33	8	.
<i>Empetrum nigrum</i>	.	.	.	8	.	.
<i>C-Agropyro-Rosetum rugosae</i>						
<i>Rosa rugosa</i>	.	.	.	.	.	100 ⁵
<i>D-Agropyro-Rosetum rugosae</i>						
<i>Chamaenerion angustifolium</i>	.	.	.	.	.	58
<i>Calamagrostis epigeios</i>	.	.	.	.	.	50
Companion taxa						
<i>Ceratodon purpureus</i>	.	37	44	50	92	.
<i>Carex arenaria</i>	.	50	9	25	33	67
<i>Cornicularia aculeata</i>	.	25	.	.	.	.
<i>Lysimachia vulgaris</i>	.	.	.	+	25	.
<i>Lythrum salicaria</i>	.	.	.	.	17	.
<i>Betula pubescens</i> juv.	.	.	9	25	17	.
<i>Pinus sylvestris</i> juv.	.	.	+	25	+	.
<i>Polytrichum formosum</i>	.	.	.	8	33	.
<i>Agropyron repens</i>	.	.	9	.	.	17
<i>Cetraria glauca</i>	.	.	27	.	.	.
<i>Cladonia chlorophaea</i> coll.	.	.	.	.	17	.
<i>Deschampsia flexuosa</i>	.	.	.	.	.	17

Occasional taxa

Brachythecium albicans 2(13), 3(9); *Cladonia cenomyce* indet. 2(13), 3(9); *Lotus corniculatus* 2(13), 4(8); *Pleurozium schreberi* 3(9), 5(8); *Viola canina* var. *denensis* 2(13); *Usnea hirta* 2(13); *Evernia prunastri* 2(+), 3(9); *Agrostis canina* 4(8); *Campyllum polygamum* 4(8); *Erica tetralix* 4(8); *Hieracium pilosella* 4(8); *Polytrichum piliferum* 4(8); *Pohlia nutans* 5(8); *Potentilla palustris* 5(8); *Agrostis tenuis* 6(8); *Myrica gale* 2(+), 4(+); *Plantago maritima* 2(+); *Salix cinerea* juv. 3(+); *Juncus bufonius* 4(+).

Location of the stands

1-3 *Ammophila arenaria* subass., T8-1970-8 (Stand 1), just behind the seaward dunes, near a small depression, UC 73807042.

2-3 *Corynephorus canescens* variant, Ha-1965-7 (Stand 2), the small slope, just behind the seaward dunes, UC 58408697. T8 1965-6 (Stand 3), on the seaward dunes, UC 73797027.

4-5 *Carex nigra* subass., T8-1967-7 (Stand 4), a small depression behind the seaward dunes, UC 73827044. T8-1966-8 (Stand 5), a small depression behind the seaward dunes, UC 73817040.

6 *Agropyro - Rosetum rugosae*, Xh-1970-6, on the low seaward dunes, UC 64203430.

Table IX. *Salici-Empetretum* (1-18); *Calluna vulgaris* sociation (19-22)

Stand No	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Number of samples	12	12	12	8	10	12	12	12	12	11	12	12	11	10	12	12	12	12	10	12	12
<i>C-Salici-Empetretum</i> et <i>Empetrium nigrum</i>	100 ⁵	100 ⁴	100 ⁴	100 ⁴	100 ⁴	33	67	58 ³	83 ³	82 ²	100 ⁴	92 ⁵	100 ³	100 ³	100 ³	92 ³	25 ²	83	.	.	.
<i>D-Festuca arenaria</i> subsp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Festuca arenaria</i>	.	100	92	87	.	8	17	.	.	.	.	.	.	36	.	.	.	.	.	.	.
<i>Viola canina</i> var. <i>denensis</i>	8	42	+	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Artemisia campestris</i>	.	25	42	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>D-Polypodium vulgare</i> subsp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Polypodium vulgare</i>	.	.	.	.	90 ²	83 ²	100 ²	17	50	.	.	.	.	.	.	.	.	.	.	.	.
<i>Amphiphila x baltica</i>	.	.	.	.	60	50 ³	42	.	.	.	8	.	.	.	.	.	.	.	.	.	.
<i>Polytrichum juniperinum</i>	.	.	.	.	.	42 ²	17	33	.	.	.	.	9	.	.	.	.	.	.	.	.
<i>Hypochoeris radicata</i>	.	.	.	.	.	17	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>D-Lophocolea heterophylla</i> subsp.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Lophocolea heterophylla</i>	.	.	.	.	.	.	.	.	.	.	.	33	18	70	8	25	.	25	.	33	.
<i>Lotus corniculatus</i>	8	.	.	.	.	.	.	.	.	.	.	.	55	.	42	.	8	42	.	.	.
<i>Pinus sylvestris</i> juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Erica tetralix</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plants common to <i>Salici-Empetretum</i> and <i>Calluna vulgaris</i> sociation	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Dicranum scoparium</i>	.	.	+	.	80 ²	100 ³	92 ³	83 ³	83 ³	100	58	67	82 ²	30	33	75	8	8	+	17	33
<i>Pleurozium schreberi</i>	.	.	+	.	80	33 ²	92 ³	50 ³	58 ²	.	8 ²	100	55 ²	100 ⁴	100 ⁴	100 ²	100 ²	8 ²	8 ²	100 ⁴	100 ³
<i>Cladonia arbuscula</i> et <i>mitis</i>	.	8	.	.	.	42	8	75	92 ²	73	100 ²	100	64	30	75	58	50	58	40	17	17
<i>C. chlorophaea</i> coll.	.	.	.	.	.	92	58	75	75 ³	82 ²	75	42	44	30	25	33	17	67	10	58	8
<i>C. implexa</i>	.	.	.	.	.	83	42	75	100 ³	91 ²	100 ⁴	100 ³	91 ²	20	67	100 ³	17	8	10	58	8
<i>Dicranum undulatum</i>	.	.	.	.	.	25	75	33	50	18	.	.	44	30	50	33	17	8	.	58	25
<i>D-Vaccinio-Genistetalia</i> et <i>Nardo-Callunetia</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Calluna vulgaris</i>	.	+	.	50	10 ²	33	42	100 ⁴	100 ⁴	9	58 ³	.	100 ³	100 ⁴	100 ³	100 ⁴	100 ⁵	100 ⁴	100 ⁵	100 ⁵	100 ⁵
<i>Hyppnum ericetorum</i>	.	.	.	.	20	.	17	25	27	.	58	36	.	75	33	75	100 ²	30	83	67	.
<i>Salix arenaria</i>	.	+	.	100 ⁴	.	8	100 ³	17	.	.	50	.	.	.	.	.	.	.	.	.	.
<i>Luzula campestris</i>	.	.	.	.	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>L. multiflora</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.
<i>Lycopodium clavatum</i>	.	.	.	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Arctostaphylos uva ursi</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Hypochoeris maculata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companion taxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Carex arenaria</i>	100	25	25	87	80	100	100	67	50	100	33	+	82	100	100	92	100	58	.	8	8
<i>Cornicularia aculeata</i>	.	42	92	.	20	8	.	25	42	64	83	17	36	.	8	.	17	8	20	.	.
<i>Corynephorus canescens</i>	.	83	67	25	20	42	17	8	25	.	42	.	9	.	.	.	.	.	.	.	.
<i>Hieracium umbellatum</i> ssp.	.	92	83	.	10	50	92	8	33	.	.	.	.	.	.	17	.	.	.	.	.
<i>Polytrichum piliferum</i>	.	25	83	.	20	17	.	.	.	.	36	58	.	.	.	.	.	.	.	.	.
<i>Jasione montana</i> var. <i>littoralis</i>	.	75	33	13	.	33	67	+	.	.	.	.	9	.	.	.	.	.	.	.	.
<i>Cladonia furcata</i>	.	.	33	.	20	8	67	.	8	.	.	.	18	.	.	.	.	.	60	.	.
<i>Ceratodon purpureus</i>	.	.	8	25	.	.	.	25	.	18	25	.	.	.	.	.	.	.	.	.	.
<i>Cladonia alpicornis</i>	.	.	.	.	.	.	.	17	.	36	17	.	.	.	.	.	.	.	.	.	.
<i>Koeleria glauca</i>	.	.	.	.	.	.	33	8	+	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cladonia cornuta</i> et <i>gracilis</i>	.	.	.	.	.	67	25	67	50	36	50	58	36	10	8	.	.	.	80	.	.
<i>C. rangiferina</i>	.	.	.	.	.	8	.	.	+	27	.	33	.	.	.	.	.	.	33	17	.
<i>Cetraria islandica</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	83	.	90	.	.
<i>Vaccinium vitis-idaea</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	33	.	.	.
<i>Quercus robur</i> juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	+	75	25
<i>Betula verrucosa</i> juv.	.	.	.	.	.	50 ³	+	+	.	.	.	.	.	.	.	+	+	.	+	+	.
<i>Vicia cracca</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.
<i>Carex panicea</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42	.	.	.
<i>Parnelia physodes</i>	.	33	83	25	10	100 ²	58	58	58	44	67	75	64	100	83	75	100	75	30	67	.
<i>Pohlia nutans</i>	.	.	.	.	.	75	25	8	42	36	25	33	36	40	8	33	.	17	.	.	.
<i>Cephalozia</i> sp.	.	.	.	.	.	17	25	58	50	27	17	8	27	.	.	17	.	.	17	.	.
<i>Amphiphila arenaria</i>	.	17	25	25	40	83	.	8	17	18	+	.	9	.	.	8	.	.	.	.	.
<i>Cladonia cenomyce</i> indet.	.	.	.	.	.	33	25	58	17	27	.	.	27	10	17	17	.	50	.	.	.
<i>Brachythecium rutabulum</i>	.	.	.	.	.	.	42	8	8	27	.	.	17	.	10	.	42	17	.	92	67
<i>Cetraria glauca</i>	.	.	.	.	.	33	8	25	8	.	.	.	.	.	.	.	.	33	.	.	.
<i>Calamagrostis epigeios</i>	.	.	37	.	.	.	.	+	8	.	.	.	27	.	.	.	.	.	+	8	.
<i>Cladonia cornutoradiata</i>	.	.	.	.	.	58	8	.	.	.	.	8	.	.	8	.	8	.	10	.	.
<i>C. uncialis</i>	.	.	.	.	.	8	.	8	8	36	.	.	.	.	.	.	8	.	10	.	.
<i>C. squamosa</i>	.	.	.	.	.	50	17	42	.	.	.	.	.	.	.	8	.	8	60	.	.
<i>C. pleurota</i>	.	.	.	.	.	33	8	33	.	9	.	.	.	.	.	.	.	.	.	.	.
<i>C. floerkeana</i>	.	.	.	.	.	.	.	.	25	9	17	.	.	.	.	25	.	.	.	.	.
<i>Galium verum</i>	.	.	.	.	10	.	58	.	.	.	.	.	.	20	.	.	.	.	.	.	.
<i>Polytrichum formosum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	58	.	.	.
<i>Drepanocladus exannulatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42	.	.	.
<i>Plantago maritima</i>	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Honkenya peploides</i>	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Occasional taxa

Rumex tenuifolius 5(8), 13(+), 14(+), 17(8); *Lophocolea bidentata* 7(8), 13(9), 20(8); *Campula rotundifolia* 12(8), 13(9), 19(+); *Scleropodium purum* 6(+), 7(8), 16(17); *Agrostis tenuis* 5(+), 13(27), 14(+); *Thymus serpyllum* 1(8), 13(9); *Poa pratensis* 5(8), 16(8); *Cladonia fimbriata* 6(25), 19(10); *Ptilidium ciliare* 8(8), 9(17); *Hylocomium splendens* 14(10), 18(8); *Peltigera malacea* 13(9), 18(25); *Anthyllis vulneraria* ssp. *maritima* 3(+), 13(18); *Deschampsia flexuosa* 7(+), 20(8); *Aira praecox* 5(10); *Elymus arenarius* 6(17); *Rhacomitrium canescens* 11(8); *Peltigera canina* 11(8); *Melampyrum pratense* 16(25); *Chamaenerion angustifolium* 17(9); *Vaccinium uliginosum* 18(25); *Parnelia furfuracea* 18(17); *Festuca ovina* 19(10); *Cladonia crispata* 19(10); *Convallaria majalis* 21(8); *Viola tricolor* ssp. *curtisii* 2(+), 6(8); *Betula pubescens* juv. 6(+); 11(+); *Knautia arvensis* 9(+), 19(+); *Festuca polesica* 8(+), 12(+); *Lathyrus maritimus* 12(+), 21(8); *Juniperus communis* 14(+), 17(+); *Populus tremula* juv. 20(+), 22(+); *Pinus mugo* juv. 1(+); *Cerastium semidecandrum* coll. 5(+); *Aulacomnium androgynum* 6(+); *Barbilophozia hatcheri* 7(+); *Helichrysum arenarium* 7(+); *Pimpinella saxifraga* 9(+); *Agrostis canina* 14(+); *Picea glauca* juv. 17(+); *Molinia coerulea* 19(+); *Viola canina* 19(+); *Geranium sanguineum* 20(+); *Lathyrus montanus* 20(+); *Peucedanum oreoselinum* 20(+).

Location of the stands

1 *Salici-Empetretum* (*Empetrium nigrum* sociation), Ha-1970-7, on the seaward dunes, S of the small river Skintan, UC 5838860.

2-4 *Festuca arenaria* subsp., Tö-1965-7 (Stand 2), on the seaward dunes, N parts, UC 75607265. Tö-1966-9 (Stand 3), on the seaward dunes, N parts, UC 73607273. Tö-1971-9 (Stand 4), on the seaward dunes, N parts, near the river Genevadsån, UC 73737233.

5-9

Polypodium vulgare subsp., Fa-1972-7 (Stand 5), the spit of Falsterbo, just behind the low seaward dunes, S side, UB 61703940. Sh-1970-10 (Stand 6), on the seaward dunes, third dune row, SW of the lighthouse, VB 48353765. Sh-1970-10 (Stand 7), the seaward dunes, third dune row, SW of the lighthouse, VB 47703755. Sh-1965-8 (Stand 8), behind the seaward dunes, SW of the lighthouse, VB 48503775. Sh-1965-8 (Stand 9), behind the seaward dunes, SW of the lighthouse, VB 48483780.

10-18

Lophocolea heterophylla subsp., Tö-1965-6 (Stand 10), on the seaward dunes, S parts, near the flat wide depression, UC 73977023. Tö-1967-10 (Stand 11), on the seaward dunes, near a small depression, S parts, UC 73837048. Sh-1967 (Stand 12), behind the seaward dunes, SW of the lighthouse, VB 48503785. Tö-1965-7 (Stand 13), on the seaward dunes, N parts, near the river Genevadsån, UC 73687280. Tö-1967-9 (Stand 14), on the seaward dunes, N parts, near the river Genevadsån, UC 73697272. Sh-1965-8 (Stand 15), behind the low seaward dunes, UC 64033390. Sh-1965-9 (Stand 16), a small dry depression, behind the low seaward dunes, VB 46803733. Sh-1970-6 (Stand 17), behind the low seaward dunes, UC 63803375. Ha-1965-7 (Stand 18), behind the seaward dunes and the flat wide depression, S of the small river Skintan, UC 58458738.

19-22

Calluna vulgaris sociation, Revingshejd-1970-9 (Stand 19), on a small sandy hill 05017582. Sh-1970-7 (Stand 20), the inner dunes, between the lighthouse and the small river Tygeån, VB 48303801. Sh-1970-7 (Stand 21), the inner dunes, between lighthouse and the small river Tygeån, VB 48253835. Sh-1970-7 (Stand 22), the inner dunes, between the lighthouse and the small river Tygeån, VB 47953820.

Table X. *Agrostio-Callunetum* (1-4)

Stand No	1	2	3	4
Number of samples	12	12	12	10
D-Agrostio-Callunetum				
<i>Hieracium pilosella</i>	50	17	100	60 ²
<i>Agrostis tenuis</i>	92	50	42	40
<i>Jasione montana</i>	33	17	25	10
<i>Knautia arvensis</i>	8	17	25	10
<i>Rumex tenuifolius</i>	17	.	25	40
<i>Hieracium umbellatum</i>	17	8	25	.
<i>Viola canina</i>	.	33	25	10
<i>Cladonia rangiferina</i>	.	50	33	.
<i>Scleranthus perennis</i>	17	.	58	.
<i>Euphorbia cyparissias</i>	.	.	50	.
<i>Hypericum perforatum</i>	42	.	.	.
C-Euphorbio-Callunetum, Vaccinio-Genistetalia et Nardo-Callunetum				
<i>Calluna vulgaris</i>	100 ⁴	100 ⁵	100 ⁵	100 ⁵
<i>Hypnum ericetorum</i>	58	100 ²	33	+
<i>Luzula campestris</i>	58	50	.	.
Companion taxa				
<i>Cladonia arbuscula</i> et <i>mitis</i>	17	33	42	10
<i>C. cornuta</i> et <i>gracilis</i>	17	17	25	40
<i>Pinus sylvestris</i> juv.	+	8	50	20
<i>Cladonia impepa</i>	33	.	17	.
<i>Cladonia furcata</i>	92	75	33	70
<i>Agrostis canina</i> ssp. <i>montana</i>	.	67	42	20
<i>Polytrichum piliferum</i>	25	67	.	.
<i>Carex arenaria</i>	.	25	67	.
<i>Campanula rotundifolia</i>	.	.	83	.
<i>Pleurozium schreberi</i>	100 ³	75 ²	92 ²	50
<i>Cladonia chlorophaea</i> coll.	17	33	25	100
<i>Lophocolea heterophylla</i>	17	25	42	100
<i>Cladonia degenerans</i>	42	25	42	30
<i>Dicranum scoparium</i>	58	.	92	90
<i>Parmelia physodes</i>	42	82	.	100
<i>Polytrichum juniperinum</i>	+	50	42	10
<i>Brachythecium rutabulum</i>	25	.	82	50
<i>Cephaloziella</i> sp.	.	92	33	30
<i>Cladonia fimbriata</i>	67	67	25	30
<i>C. squamosa</i>	17	.	.	80
<i>Festuca ovina</i>	33	17	.	.
<i>Galium verum</i>	.	+	67	.
<i>Cladonia cornutoradiata</i>	.	67	.	.
<i>Pohlia nutans</i>	.	.	.	60
<i>Peltigera canina</i>	.	.	25	.
<i>Carex hirta</i>	.	42	.	.
<i>Cladonia elongata</i>	33	.	.	.

Occasional taxa

Artemisia campestris 2(8), 3(+), 4(10); *Cladonia glauca* 1(25), 4(10); *C. pleurota* 2(8), 3(8); *Scleropodium purum* 2(8), 3(17); *Quercus robur* juv. 1(17), 2(+); *Thymus serpyllum* 2(25), 3(+); *Festuca rubra* 1(+), 4(10); *Deschampsia flexuosa* 2(+), 4(30); *Aira praecox* 1(17); *Anthoxanthum odoratum* 1(17); *Hypochoeris radicata* 1(17); *Teesdalia nudicaulis* 1(17); *Pimpinella saxifraga* 3(17); *Ceratodon purpureus* 4(10); *Holcus mollis* 4(10); *Lophocolea bidentata* 4(10); *Achillea millefolium* 1(8); *Luzula pilosa* 1(8); *Veronica chamaedrys* 1(8); *Cladonia cernomyces* indet. 2(8); *Anthyllis vulneraria* 2(8); *Dicranum undulatum* 4(8); *Corynephorus canescens* 1(+); *Rhacomitrium canescens* 1(+); *Ononis repens* 2(+); *Ptilidium ciliare* 2(+); *Cerastium arvense* 3(+).

Location of the stands

1-4 *Agrostio-Callunetum*, Björka-1967-7 (Stand 1), glaci-fluvial sandy hill, near the small river Björkaån, VB 15106838. Vitaby-1965-9 (Stand 2), glaci-fluvial sand, between the church and Vitabilla, VB 48557303. Vomb-1967-8 (Stand 3), glaci-fluvial sand, between the church and the river Klingavälsån, VB 08307195. Hemmestorp-1971-10 (Stand 4), glaci-fluvial sand, near a sand pit, VB 09656492.

Table XII. *Cladonio - Pinetum sylvestris* (1-3)

Stand No	1	2	3
Number of samples	8	12	12
C-Cladonio - Pinetum sylvestris et Cladonio-Pinion			
<i>Cladonia arbuscula</i> et <i>mitis</i>	100 ²	100 ²	50
<i>C. impepa</i>	100 ³	100 ⁴	25
<i>C. cornuta</i> et <i>gracilis</i>	87 ²	58	42
<i>C. rangiferina</i> (D-subass.)	100 ²	17	.
D-Corynephorus canescens subass.			
<i>Corynephorus canescens</i>	+	50	75
<i>Cornicularia aculeata</i>	.	50	50
<i>Carex arenaria</i>	13	17	75
<i>Cladonia furcata</i>	.	8	58
<i>Polytrichum piliferum</i>	.	17	.
D-Galium verum variant			
<i>Galium verum</i>	.	.	58
<i>Ammophila arenaria</i>	.	.	42
C-Vaccinio-Piceetalia et Vaccinio-Piceetalia			
<i>Pinus sylvestris</i>	100 ⁴	42 ²	58 ³
<i>Dicranum undulatum</i>	62	83	67 ³
<i>Pinus sylvestris</i> juv.	25	100	+
Companion taxa			
<i>Pleurozium schreberi</i>	25	50	100 ³
<i>Dicranum scoparium</i>	100	58	50 ²
<i>Cladonia chlorophaea</i> coll.	87	67	50
<i>Deschampsia flexuosa</i>	62	.	100
<i>Pohlia nutans</i>	.	42	17
<i>Cladonia fimbriata</i>	.	.	33
<i>Hieracium umbellatum</i> ssp.	.	8	17
<i>Hypnum cupressiforme</i> coll.	25	8	.

Occasional taxa

Cladonia degenerans 2(17); *C. uncialis* 2(17); *C. floerkeana* 3(17); *Parmelia physodes* 3(17); *Cephaloziella* sp. 3(17); *Calluna vulgaris* 1(13); *Betula pubescens* juv. 1(13); *Brachythecium rutabulum* 1(13); *Ceratodon purpureus* 2(8); *Empetrum nigrum* 2(8); *Polypodium vulgare* 2(8); *Polytrichum juniperinum* 2(8); *Cladonia cornutoradiata* 3(8); *C. squamosa* 3(8); *Parmelia furfuracea* 3(8); *Usnea hirta* 3(8); *Juniperus communis* 2(+); *Luzula campestris* 2(+); *Pinus mugo* 2(+); *Rumex tenuifolius* 2(+); *Betula verrucosa* juv. 3(+); *Festuca polesica* 3(+); *Populus tremula* juv. 3(+); *Salix caprea* juv. 3(+); *Viola canina* var. *dimensis* 3(+).

Location of the stands

- 1 Typical (*Cladonia rangiferina*) subass., Sh-1971-8, rarely in the dunes often adjacent to *Vaccinio-Pinetum*, VB 46203780.
- 2-3 *Corynephorus canescens* subass., Tö-1970-8 (Stand 2), the inner dune ridges, ca. 3 km from the seashore, UC 76356970.
- 3 *Galium verum* variant, Fb-1965-9, just behind the seaward dunes before the flat sandy plain, UC 51158747.

Table XI. *Molinio - Myricetum gale* (1-7)

Stand No	1	2	3	4	5	6	7
Number of samples	12	12	8	12	12	12	12
<i>C-Molinio - Myricetum gale</i>							
<i>Myrica gale</i>	+	67 ²	100 ²	100 ²	92 ³	100 ³	.
<i>D-Salix arenaria</i> subass.							
<i>Salix arenaria</i>	100 ²	100 ²	100 ³	100 ³	33 ³	25	.
<i>D-variants</i>							
<i>Vaccinium uliginosum</i>	100 ⁵	50	.	58	.	.	.
<i>Potentilla erecta</i>	83	.	.	+	.	.	.
<i>Festuca arenaria</i>	33	.	.	.	.	.	.
<i>Erica tetralix</i>	.	100 ⁴	37 ²	.	+	.	.
<i>Cephaloziella</i> sp.	.	92	.	.	.	.	.
<i>Peltigera malacea</i>	.	75	.	.	.	.	.
<i>Empetrum nigrum</i>	.	67 ²	.	.	.	.	.
<i>Gymnocolea inflata</i>	.	58 ²	13	.	.	.	.
<i>Calluna vulgaris</i>	.	58	.	.	.	.	8
<i>Luzula multiflora</i>	.	42	.	.	.	.	.
<i>Sphagnum recurvum</i>	.	.	100 ²	+	.	.	.
<i>Oxycoccus palustris</i>	.	.	87	8	.	.	.
<i>Viola palustris</i>	.	.	87	.	.	.	.
<i>Agrostis canina</i>	.	.	.	75	.	8 ⁴	.
<i>Potentilla palustris</i>	.	.	25	58	.	8 ⁴	.
<i>Lysimachia vulgaris</i>	.	.	.	.	58 ²	33	.
<i>Lythrum salicaria</i>	.	.	.	.	75 ⁴	17 ⁴	.
<i>Carex acuta</i>	.	.	.	.	42	33	.
<i>D-dominant Molinia coerulea</i> soc.							
<i>Molinia coerulea</i>	.	.	100 ⁴	+	.	.	100 ⁵
<i>Companion taxa</i>							
<i>Carex nigra</i>	58	75	37	100 ³	75 ³	75 ³	8
<i>Drepanocladus exannulatus</i>	50	75	.	58	.	.	.
<i>Calliergon cordifolium</i>	.	.	.	75	.	58	.
<i>Carex canescens</i>	.	.	.	.	.	58	.
<i>Juncus filiformis</i>	.	.	.	.	33 ³	.	.
<i>Galium uliginosum</i>	17	.	.	75	83	92	.
<i>Carex panicea</i>	.	92	.	58	.	.	.
<i>Juncus conglomeratus</i>	.	.	.	.	.	42	.
<i>Scutellaria galericulata</i>	.	.	.	.	92	.	.
<i>Lycopus europaeus</i>	.	.	.	.	25 ³	.	.
<i>Iris pseudacorus</i>	.	.	.	.	17 ²	.	.
<i>Sieglingia decumbens</i>	42	+	13	.	17 ²	.	.
<i>Aulacomnium palustre</i>	33	17	.	17	.	.	.
<i>Dicranum scoparium</i>	.	33	.	.	.	.	58
<i>Pohlia nutans</i>	33	33	.	.	.	.	.
<i>Lophocolea heterophylla</i>	.	50	.	17	.	.	.
<i>Carex arenaria</i>	17	33	.	.	.	.	.
<i>Cladonia chlorophaea</i> coll.	.	33 ²	.	.	.	.	8
<i>Hypnum cupressiforme</i> coll.	.	8 ²	.	.	.	.	25
<i>Calamagrostis epigeios</i>	.	.	.	+	.	33	.
<i>Brachythecium rutabulum</i>	.	.	.	.	.	.	42
<i>Salix cinerea</i>	.	.	.	.	.	33	.
<i>Cladonia cenomyce</i> indet.	.	33	.	8	.	.	.
<i>Deschampsia flexuosa</i>	.	.	.	.	.	.	25

Occasional taxa

Potentilla anserina 1(17), 4(8³); *Parmelia physodes* 2(17), 4(+); *Polytrichum formosum* 1(8), 2(8); *Cladonia impexa* 2(8), 7(8); *Campylopus polygamus* 5(8), 6(+); *Betula pubescens* juv. 1(8), 4(+); *Naumburgia thyrsiflora* 4(+), 5(+); *Achillea millefolium* 1(17); *Galium verum* 1(17); *Cladonia arbuscula* et *mitis* 7(17); *Veronica scutellata* 5(17); *Achillea ptarmica* 5(17); *Fillipendula ulmaria* 1(8); *Viola canina* 1(8); *Cladonia* cf. *strepsilis* 2(8); *Cladonia* cf. *degenerans* 2(17); *Polytrichum piliferum* 2(8); *Cladonia floerkeana* 2(8); *Polytrichum commune* 7(8); *Polygonum amphibium* 5(8); *Lycopodium inundatum* 5(8); *Juncus effusus* 6(8²); *Phragmites communis* 6(+); *Quercus robur* juv. 7(8).

Location of the stands

- 1-6 *Salix arenaria* subass., Ha-1970-7 (Stand 1 = *Vaccinium uliginosum* variant), the flat wide depression, just behind the seaward dunes, periodically inundated, UC 58318695.
- 2 *Erica tetralix* variant, Ha-1965-7, the flat wide depression, inland from the seaward dunes, periodically inundated, UC 58338697.
- 3 *Oxycoccus palustris* variant, Ha-1971-8, the flat wide depression, inland from the seaward dunes, periodically inundated, UC 58338693.
- 4 *Agrostis canina* variant, Ha-1965-7, the flat wide depression, inland from the seaward dunes, near a ditch, periodically inundated, UC 58348697.
- 5-6 *Carex acuta* variant, T8-1967-7 (Stand 5), the small depression, behind the seaward dunes connected with the flat wide depression, periodically inundated, UC 73857050. T8-1965-7 (Stand 6), a corner of the flat wide depression, periodically inundated, UC 73887080.
- 7 *Molinia coerulea* sociation, Sh-1970-7, small low parts of the inner dunes; often surrounded with dwarf shrubs, VB 48303832.

Table XIII. *Vaccinio - Pinetum sylvestris* (1-4); *Deschampsia flexuosa - Pinus sylvestris* community (5-7)

Stand No	1	2	3	4	5	6	7
Number of samples	12	12	12	10	12	12	8
<u>Local C-Vaccinio - Pinetum sylvestris</u>							
<i>Hylocomium splendens</i>	92 ³	25 ²	75	40 ²	.	.	..
<i>D-Empetrum nigrum subass.</i>							
<i>Empetrum nigrum</i>	100 ³	100 ⁴	92 ²	.	.	.	.
<i>D-Quercus petraea subass.</i>							
<i>Quercus petraea</i>	.	.	.	40 ⁵	.	.	.
<i>Q. petraea juv.</i>	.	.	.	30	.	.	.
<i>Picea abies</i>	.	.	.	20	.	.	.
<i>D-Calluna vulgaris variant</i>							
<i>Calluna vulgaris</i>	.	92 ²	100 ⁴	+	8	8	.
<i>Parmelia physodes</i>	.	17	67	.	.	.	.
<i>Cladonia arbuscula et mitis</i> (C-high order)	.	25	33	.	.	.	.
<u>Local D-Deschampsia flexuosa - Pinus sylvestris community</u>							
<i>Deschampsia flexuosa</i>	.	+	.	10	100	100 ⁵	100 ⁴
<u>D-variants</u>							
<i>Lophocolea bidentata</i>	.	.	.	.	17	67	.
<i>Melampyrum pratense</i>	.	.	.	8	.	.	87
<i>Polypodium vulgare</i>	.	.	.	.	+	.	75 ²
<i>Luzula campestris</i>	.	.	.	.	.	8	75
<u>C-Vaccinio-Pinion</u>							
<i>Dicranum undulatum</i>	100 ⁴	67 ²	83 ⁴	80 ²	83 ³	50	25
<u>C-Vaccinio-Piceetalia et Vaccinio-Piceetea</u>							
<i>Pinus sylvestris</i>	100 ³	67 ²	75 ²	100 ³	100 ⁴	100 ³	87 ⁴
<i>Vaccinium vitis-idaea</i>	100 ⁴	+	100 ²	100 ³	.	.	62
<i>Trientalis europaea</i>	.	+	.	.	.	.	50
<i>Cladonia impexa</i>	.	.	17	.	.	.	.
<i>Pinus sylvestris juv.</i>	8 ²	+	+	.	.	.	.
<i>Ptilium crista-castrensis</i>	8 ²	.	.	+	.	.	.
<i>Vaccinium myrtillus</i>	.	.	.	10	.	.	+
<i>Cladonia rangiferina</i>	.	.	8	.	.	.	.
<u>Companion taxa</u>							
<i>Pleurozium schreberi</i>	100 ²	100 ³	100 ⁴	100 ⁴	100 ⁵	100 ²	100 ⁵
<i>Carex arenaria</i>	83	100 ²	100	20	33 ²	8	87
<i>Hypnum cupressiforme coll.</i>	.	83	42	60	33 ²	8	.
<i>Brachythecium rutabulum</i>	.	.	67	50	33	25	50
<i>Dicranum scoparium</i>	.	17	.	40	42	50	.
<i>Scleropodium purum</i>	8	25	.	40	8	.	50
<i>Lophocolea heterophylla</i>	.	.	25	30	.	.	.
<i>Cladonia cenomyce indet.</i>	.	8	33	.	.	.	.
<i>Quercus robur juv.</i>	.	+	.	.	+	17	+
<i>Plagiothecium sp.</i>	.	.	.	30	.	.	.

Occasional taxa

Betula pubescens juv. 1(8), 2(+), 3(+), 4(20); *Sorbus aucuparia* juv. 3(+), 7(13); *Betula verrucosa* juv. 2(8), 3(+); *Vaccinium uliginosum* 1(+), 4(10); *Erica tetralix* 3(17); *Luzula pilosa* 7(25); *Betula pubescens* 4(10); *Cephalozia* sp. 3(8); *Hieracium* sp. 6(8); *Ptilidium ciliare* 3(8); *Salix arenaria* 1(+), 2(+), 3(+); *Festuca arenaria* 2(+); *Luzula multiflora* 2(+); *Myrica gale* 3(+); *Populus tremula* juv. 3(+); *Juniperus communis* 4(+); *Dryopteris spinulosa* 7(+).

Location of the stands

- 1-3 *Empetrum nigrum subass.*, Tö-1970-8 (Stand 1), near the inner dune ridges, ca. 3 km from the seashore, UC 76106965.
- 2-3 *Calluna vulgaris variant*, Åh-1965-8 (Stand 2), inland from the seaward dunes, UC 64103355. Tö-1967-10 (Stand 3), near the motorway on the coastal side, UC 74237075.
- 4 *Quercus petraea subass.*, Ha-1971-8, just below the highest point of Lynga dune, UC 59408765.
- 5-6 *Lophocolea bidentata variant*, Sh-1967-11 (Stand 5), the inner dunes, VB 48083813. Sh-1970-7 (Stand 6), inner dunes, VB 48063813.
- 7 *Polypodium vulgare variant*, Fb-1970-7, slope of the row of high dunes, inland from the sandy plain, VB 50908775.

Table XIV. *Agrostis tenuis*-*Populus tremula* community (1); *Oxalis acetosella*-*Quercus petraea* community (2); *Melampyro-Quercetum roboris* *Calamagrostis epigaeos* vicariant (3-10)

Stand No	1	2	3	4	5	6	7	8	9	10
Number of samples	8	12	12	12	12	12	10	6	6	6
<u>C-dominant <i>Agrostis tenuis</i>-<i>Populus tremula</i> community</u>										
<i>Populus tremula</i> (tall shrub)	100 ⁵	.	.	.	.	.	.	.	.	.
<u>D-<i>Agrostis tenuis</i>-<i>Populus tremula</i> community</u>										
<i>Lophocolea bidentata</i>	100	.	.	.	.	.	.	.	.	.
<i>Agrostis tenuis</i>	87	.	+	.	.	.	.	17	.	.
<i>Rubus idaeus</i>	37	.	.	.	.	.	.	.	.	.
<u>Local C-<i>Oxalis acetosella</i>-<i>Quercus petraea</i> community</u>										
<i>Quercus petraea</i>	.	100 ⁵	.	.	.	.	.	.	.	.
<i>Sorbus aucuparia</i>	.	100 ⁴	.	.	.	.	.	.	.	.
<i>Quercus petraea</i> juv.	.	17	.	.	.	.	.	.	.	.
<u>D-<i>Oxalis acetosella</i>-<i>Quercus petraea</i> community</u>										
<i>Oxalis acetosella</i>	.	100 ⁵	.	.	.	.	.	.	.	.
<i>Anemone nemorosa</i>	.	x ⁸	.	.	.	.	.	.	54	.
<i>Fragaria vesca</i>	.	50	.	.	.	.	.	.	.	.
<i>Poa nemoralis</i>	.	42	.	.	.	.	.	.	.	.
<i>Brachythecium velutinum</i>	.	42	.	.	.	.	.	.	.	.
<u>D-<i>Melampyro-Quercetum roboris</i></u>										
<i>Calamagrostis epigaeos</i> (coastal vic.)	.	.	100 ²	42	+	33	+	100 ²	100	17
<u>D-<i>Corylus avellana</i> subass.</u>										
<i>Corylus avellana</i>	.	8 ²	.	.	.	.	.	.	100 ³	.
<i>Rhamnus frangula</i>	25	.	.	.	.	+	+	.	84 ³	.
<u>D-<i>Corynephorus canescens</i> subass.</u>										
<i>Corynephorus canescens</i>	.	.	.	.	.	.	.	.	.	100
<i>Cladonia chlorophaea</i> coll.	.	.	.	.	.	.	.	.	.	100
<i>Cornicularia aculeata</i>	.	.	.	.	.	.	.	.	.	34
<i>Polytrichum piliferum</i>	.	.	.	.	.	.	.	.	.	34
<u>D-variants</u>										
<i>Luzula campestris</i>	.	.	.	42	25	.	.	.	.	.
<i>Anthoxanthum odoratum</i>	13	.	+	17	50	.	.	.	.	.
<i>Vaccinium myrtillus</i>	.	.	.	.	100 ⁵	.	.	.	.	.
<i>Peucedanum oreoselinum</i>	.	.	.	.	.	+	.	84 ²	.	.
<i>Vicia cassubica</i>	.	.	.	.	.	.	.	34 ⁴	.	.
<u>C-<i>Melampyro-Quercion</i>, <i>Melampyro-Quercetalia</i> et <i>Deschampsia-Quercetalia robori-petraeae</i></u>										
<i>Melampyrum pratense</i>	25	8 ²	100 ³	100 ²	33 ⁴	92	80 ²	100 ³	50 ²	+
<i>Convallaria majalis</i>	.	100 ⁵	25	100 ²	100 ⁴	50 ²	100 ⁵	100 ³	100 ⁵	67 ²
<i>Quercus robur</i>	.	.	+	100 ²	100 ⁵	100 ³	100 ⁵	100 ⁵	+	100 ²
<i>Sorbus aucuparia</i> juv.	37	33	+	.	17	17	20	.	+	.
<i>Quercus robur</i> juv.	13	.	58	8	17	25	50	.	.	.
<i>Populus tremula</i> juv.	87	+	.	25	17	60	.	.	.	84
<i>Maianthemum bifolium</i>	100 ⁵	83	.	.	+	100 ²	.	.	67 ²	.
<i>Solidago virgaurea</i>	.	17	+	.	8	.	+	.	.	.
<i>Populus tremula</i>	.	.	.	.	.	.	30 ⁴	.	.	.
<i>Betula verrucosa</i> (D-variant)	.	.	92 ⁴	.	.	+	.	.	.	.
<i>Pteridium aquilinum</i> (D-variant)	.	.	.	.	.	.	100 ⁵	.	.	.
<i>Lonicera periclymenum</i>	.	.	.	.	.	.	.	.	34 ²	.
<i>Lathyrus montanus</i>	.	.	.	.	.	8	.	.	.	.
<i>Rubus saxatilis</i>	.	.	.	.	.	8	.	.	.	.
<u>Companion taxa</u>										
<i>Carex arenaria</i>	25	17	100 ²	67	25	8	10	+	.	50
<i>Campanula rotundifolia</i>	13	.	.	.	58	.	20	67	.	17
<i>Deschampsia flexuosa</i>	87 ³	8	75 ³	100 ²	100 ⁵	100	90 ³	100 ³	84 ²	67 ²
<i>Brachythecium rutabulum</i>	87	.	92 ²	.	25	17	30	50	.	.
<i>Poa pratensis</i>	.	.	17	50	8	8	.	17	.	.
<i>Pleurozium schroberi</i>	25	.	17	.	42	.	30	.	.	.
<i>Hypnum cupressiforme</i> coll.	.	.	17	.	42	8	.	.	.	.
<i>Lysimachia vulgaris</i>	62	33	.	.	.	.	.	.	.	.
<i>Scleropodium purum</i>	.	.	33	.	.	.	10	.	.	.
<i>Dicranum scoparium</i>	.	.	.	.	50	.	.	.	.	34
<i>Rubus fruticosus</i>	.	.	.	.	.	.	.	.	50	.
<i>Festuca rubra</i>	.	.	.	8	.	.	.	50	.	.

a) *Anemone nemorosa* only in the spring.

Occasional taxa

Polygonatum odoratum 3(8), 4(8), 8(17), 9(17);
Mnium affine 1(25), 3(8), 7(10), 8(17); *Calluna vulgaris* 3(8), 5(8), 8(17); *Scorzonera humilis* 4(8), 6(8), 8(17); *Platanthera bifolia* 4(8), 5(+), 7(20); *Dryopteris spinulosa* 1(13), 2(+); *Pimpinella saxifraga* 3(8), 5(17); *Empetrum nigrum* 3(8), 5(8); *Scutellaria galericulata* 1(37); *Cladonia cornuta* et *gracilis* 10(34); *C. pleurota* 10(34); *Brachythecium albicans* 1(25); *Glechoma hederacea* 2(25); *Mnium undulatum* 2(25); *Calliergonella cuspidata* 3(25); *Ceum urbanum* 2(17); *Galium verum* 3(17); *Agrostis canina* 4(17); *Vicia cracca* 4(17); *Achillea millefolium* 5(17); *Helictotrichon pubescens* 8(17); *Rhodobryum roseum* 8(17); *Betula pubescens* juv. 1(13); *Epipactis helleborine* 3(8); *Salix arenaria* 3(8); *Lophocolea heterophylla* 5(8); *Veronica chamaedrys* 5(8); *Hylocomium splendens* 6(8); *Rhytidia delphus squarrosus* 6(8); *Lycopus europaeus* 1(+); *Mnium cuspidatum* 1(+); *Plagiothecium* sp. 1(+); *Polypodium vulgare* 1(+); *Rosa canina* 1(+); *Stellaria media* 1(+); *Veronica officinalis* 1(+); *Anthriscus sylvestris* 2(+); *Molinia caerulea* 2(+); *Alnus glutinosa* juv. 3(+); *Aulacomium androgynum* 4(+); *Campanula persicifolia* 5(+); *Dactylis glomerata* 7(+).

Location of the stands

1 *Agrostis tenuis* - *Populus tremula* community, Sh-1970-6, near the small elongated depression; between the seaward dunes and the pond, UC 64523445.

- 2 *Oxalis acetosella*-*Quercus petraea* community, Ha-1970-7, just behind the old dunes, 1.7 km from the sea-shore, UC 59968690.
- 3-8 *Melampyro-Quercetum roboris* (typical subass.), Sh-1970-7 (Stand 3 = *Betula verrucosa* variant), just behind the seaward dunes in a dry depression, SW of the lighthouse, VB 46753738.
- 4-5 *Luzula campestris* variant, Sh-1970-7 (Stand 4), the inner dunes, between the lighthouse and the small river Tygeån, VB 47605793. Sh-1967-3 (Stand 5), the inner dunes, between the lighthouse and the small river Tygeån, VB 48403801.
- 6 *Vaccinium myrtillus* variant, Sh-1970-7, the inner dunes, between the lighthouse and the small river Tygeån, VB 47703832.
- 7 *Pteridium aquilinum* variant, Sh-1971-8, the inner dunes, between the lighthouse and the small river Tygeån, VB 46703815.
- 8 *Peucedanum oreoselinum* variant, the inner dunes, between the small river Tygeån and the Käsebergaäsen esker, VB 45603815.
- 9 *Corylus avellana* subass., Sh-1970-7, the inner dunes, between the small river Tygeån and the Käsebergaäsen esker, VB 45553790.
- 10 *Corynephorus canescens* subass., Sh-1970-7, the inner dunes, between the lighthouse and the small river Tygeån, VB 47653810.

Table XV. *Agrostio - Quercetum roboris* (1-3)

Stand No	1	2	3
Number of samples	6	12	10
D-Agrostio - Quercetum roboris			
<i>Agrostis tenuis</i>	84 ²	100 ³	70
<i>Veronica chamaedrys</i>	84	8	.
<i>Galium verum</i>	50	8	.
<i>Achillea millefolium</i>	100	.	.
<i>Anthriscus sylvestris</i>	34	+	.
<i>Dactylis glomerata</i>	34	+	.
<i>Hypericum perforatum</i>	.	25	.
<i>Viola riviniana</i>	.	17	.
<i>Galeopsis tetrahit</i>	.	.	10
D-variants			
<i>Geranium sanguineum</i>	100 ²	.	.
<i>Linaria vulgaris</i>	67	.	.
<i>Corylus avellana</i>	50	.	.
<i>Festuca rubra</i>	.	100	.
<i>Anthoxanthum odoratum</i>	+	67	.
<i>Luzula campestris</i>	.	33	.
<i>Poa pratensis</i>	.	.	30 ²
<i>Rhamnus frangula</i>	.	.	30 ⁴
<i>Betula verrucosa</i>	.	.	20
C-Agrostio-Quercion, Melampyro-Quercetalia et Deschampsio - Quercetea robori - petraeae			
<i>Quercus robur</i>	50 ⁵	100 ⁵	100 ⁵
<i>Melampyrum pratense</i>	100	.	+
<i>Lonicera periclymenum</i>	.	.	80 ²
<i>Quercus robur</i> juv.	.	8	10
<i>Solidago virgaurea</i>	17	.	.
<i>Hieracium umbellatum</i>	.	17	.
<i>Populus tremula</i> juv.	+	+	+
<i>Sorbus aucuparia</i>	.	.	+
Companion taxa			
<i>Carex arenaria</i>	17	50	80
<i>Campanula rotundifolia</i>	+	33	+
<i>Agrostis canina</i> ssp. <i>montana</i>	.	17	.
<i>Deschampsia flexuosa</i>	100	+	100 ³
<i>Calamagrostis epigeios</i>	+	17	.
<i>Allium oleraceum</i>	17	.	.
<i>Hieracium pilosella</i>	17	.	.
<i>Knautia arvensis</i>	17	.	.
<i>Sedum telephium</i>	17	.	.
<i>Brachythecium rutabulum</i>	.	17	.
<i>Festuca ovina</i>	.	17	.
<i>Dicranum scoparium</i>	.	.	20
<i>Pleurozium schreberi</i>	.	.	20
<i>Pohlia nutans</i>	.	.	20

Occasional taxa

Campanula persicifolia 2(8); *Cerastium arvense* 2(8); *Luzula pilosa* 2(8); *Pimpinella saxifraga* 2(8); *Rumex tenuifolius* 2(8); *Taraxacum* sp. 2(8); *Arrhenatherum elatius* 1(+); *Agropyron repens* 1(+); *Phleum phleoides* 1(+); *Jasione montana* 2(+); *Hypnum cupressiforme* coll. 3(+); *Betula pubescens* juv. 2(+); *Juniperus communis* 3(+); *Pinus sylvestris* juv. 3(+); *Rubus fruticosus* 3(+).

Location of the stands

- Geranium sanguineum* variant, Sh-1970-7, the inner dunes adjacent to the Käsebergaäsen esker, VB 45603830.
- Festuca rubra* variant, Revingeheg-1967-8, slope of glacialfluvial sand, VB 05057572.
- Poa pratensis* variant, Hemmestorp-1971-8, glacialfluvial sand, near arable land, VB 10106440.

Table XVI. *Irido - Alnetum glutinosae* (1-4);*Filipendulo - Alnetum glutinosae* (5)

Stand No	1	2	3	4	5
Number of samples	12	10	10	8	10
C-Irido - Alnetum glutinosae et Irido - Alnion glutinosae					
<i>Solanum dulcamara</i>	.	.	50 ³	87 ²	.
<i>Carex elongata</i>	.	+	100 ³	.	.
D-Irido-Alnetum glutinosae					
<i>Iris pseudacorus</i>	75 ³	90 ³	100	75	.
<i>Peucedanum palustre</i>	42	40	80	50	10
<i>Lycopus europaeus</i>	8	60	40	75	10
D-Potentilla palustris subass.					
<i>Sphagnum recurvum</i>	42 ³	.	.	.	.
<i>Potentilla palustris</i>	33	.	.	13	.
D-Mnium punctatum subass.					
<i>Mnium punctatum</i>	.	20	90	13	.
<i>Cardamine amara</i>	.	40	80	+	.
<i>Caltha palustris</i>	.	30	40	50	10
<i>Myosotis caespitosa</i>	.	+	10	37	.
<i>Pellia epiphylla</i>	.	+	+	25	.
C-Irido - Alnetalia glutinosae et Carici - Alnetea glutinosae					
<i>Alnus glutinosa</i>	92 ⁴	100 ⁵	100 ⁵	100 ⁵	100 ⁴ a)
<i>Calamagrostis canescens</i>	83 ³	+	+	.	.
<i>Sphagnum squarrosum</i>	67 ³	.	.	.	.
<i>Stellaria longifolia</i>	.	10	.	.	.
D-Filipendulo-Alnetum glutinosae					
<i>Lythrum salicaria</i>	.	10	.	.	70 ²
<i>Scutellaria galericulata</i>	.	.	10	13	70 ²
<i>Rubus caesius</i>	.	.	.	.	60 ³
<i>Viburnum opulus</i>	.	.	.	.	30
<i>Humulus lupulus</i>	.	.	.	.	+
C-Geranio-Fraxinetea et Carpino-Fagetea					
<i>Anemone nemorosa</i>	.	.	.	+	X ⁴ b)
<i>Athyrium filix-femina</i>	.	.	40	13 ³	40 ⁴
<i>Ranunculus auricomus</i>	.	20	.	.	10
<i>Paris quadrifolia</i>	.	.	.	.	10
Companion taxa					
<i>Lysimachia vulgaris</i>	100 ²	70 ²	80	25	50 ⁴ a)
<i>Filipendula ulmaria</i>	.	30	40	25	100 ⁴
<i>Deschampsia caespitosa</i>	.	10	60	50	40
<i>Valeriana sambucifolia</i>	.	.	.	37	50
<i>Galium uliginosum</i>	.	40	10	13	.
<i>Angelica sylvestris</i>	.	.	.	25	+
<i>Galium palustre</i>	58 ³	40 ²	90	25	50
<i>Carex acuta</i>	100 ³	10 ²	+	13	.
<i>Naumburgia thyrsiflora</i>	.	60 ²	30	13	.
<i>Alisma plantago-aquatica</i>	.	10 ²	.	50	.
<i>Calliergon cordifolium</i>	58	+	70	25	.
<i>Viola palustris</i>	.	+	60	37	60
<i>Carex canescens</i>	.	40	.	.	.
<i>Calliergonella cuspidata</i>	33 ³	60 ³	100 ²	75 ²	+
<i>Betula pubescens</i>	67 ³	30 ²	.	37 ²	42 ²
<i>Mnium hornum</i>	58	30 ⁵	60	37 ²	.
<i>Chiloscyphus pallescens</i>	25	20	100	87	.
<i>Brachythecium rutabulum</i>	17	10	20	25	10
<i>B. reflexum</i>	.	+	70	50	80
<i>Lophocolea bidentata</i>	33	40	10	.	.
<i>Plagiothecium</i> sp.	17	30	80	50	.

a) In *Filipendulo-Alnetum* *Alnus glutinosa* and *Filipendula ulmaria* are dominant companion taxa.

b) *Anemone nemorosa* may be dominant in the spring.

Occasional taxa

Juncus conglomeratus 1(8), 2(10), 3(10); *Equisetum palustre* 2(20), 4(25); *Nentha arvensis* 3(30), 5(10); *Lophocolea cuspidata* 2(20), 4(13); *Stellaria media* 3(20), 4(13); *Rhamnus frangula* 2(10), 3(30); *Campyllum polygonum* 2(10), 4(13); *Rubus idaeus* 2(10), 4(13); *Juncus effusus* 2(10), 4(13); *Hypnum cupressiforme* coll. 2(+), 4(13); *Veronica scutellata* 3(30); *Haianthemum bifolium* 5(30); *Betula pubescens* juv. 2(20); *Dryopteris spinulosa* 2(20); *Salix cinerea* 1(17); *Agrostis stolonifera* 4(13); *Glyceria fluitans* 4(13); *Polygonum lapathifolium* 4(13); *Trientalis europaea* 2(10); *Rhytidia-delpheus triquetrus* 2(10); *Holcus lanatus* 2(10); *Ranunculus repens* 3(10); *Phalaris arundinacea* 5(10); *Rhytidia-delpheus squarrosus* 5(10); *Sorbus aucuparia* juv. 5(10); *Cirsium palustre* 2(+); 4(+); *Carex lasiocarpa* 1(+); *Phragmites communis* 1(+); *Carex nigra* 2(+); *Drepanocladus uncinatus* 5(+).

Location of the stands

- Potentilla palustris* subass., Sh-1971-7, inland from the seaward dunes, near a pond, adjacent to *Alno-Salicetum cinereae*, UC 64703447.
- Mnium punctatum* subass., Tö-1968-8 (Stand 2), inland from the seaward dunes, adjacent to *Alno-Salicetum cinereae*, UC 73657051. Sh-1971-8 (Stand 3), inland from the seaward dunes, near a pond, adjacent to *Alno-Salicetum cinereae*, UC 64703450. Tö-1971-9 (Stand 4), inland from the seaward dunes, adjacent to *Caricetum acutae* and *Alno-Salicetum cinereae*, UC 73657046.
- Filipendulo-Alnetum glutinosae*, Tö-1970-8, near the small river Genevadsån, on the coastal side of the motorway, UC 73967225.

Table XVII. *Myrica* - *Betuletum pubescentis* (1-2);
Polytricho - *Betuletum pubescentis* (3-5)

Stand No	1	2	3	4	5
Number of samples	8	12	12	12	10
<i>D-Myrica</i> - <i>Betuletum pubescentis</i>					
<i>Myrica gale</i>	100 ⁵	100 ³	.	.	.
<i>Dicranum undulatum</i>	50 ⁴	100 ²	.	.	.
<i>Pleurozium schreberi</i>	50	92 ³	.	.	.
<i>D-variants</i>					
<i>Betula verrucosa</i>	50 ³	100 ⁵	.	.	.
<i>Hylocomium splendens</i>	.	100 ²	.	.	.
<i>Vaccinium vitis-idaea</i>	+	83 ²	.	.	.
<i>D-Polytricho</i> - <i>Betuletum pubescentis</i>					
<i>Polytrichum commune</i>	.	.	100 ⁵	+	60 ⁴
<i>Sphagnum squarrosum</i>	.	.	17	.	60 ⁴
<i>S. fimbriatum</i>	.	.	8	.	40 ⁴
<i>D-variants</i>					
<i>Carex nigra</i>	50	58	.	100 ⁵	30
<i>Eriophorum angustifolium</i>	.	.	.	.	80 ³
<i>Sphagnum recurvum</i>	.	.	.	.	70 ³
<i>Carex rostrata</i>	.	.	.	.	40
<i>C-Molinia</i> - <i>Betuletalia pubescentis</i> <i>et Molinio</i> - <i>Betuletea pubescentis</i>					
<i>Betula pubescens</i>	50 ²	100 ⁴	100 ⁵	75 ⁴	40 ²
<i>B. pubescens</i> juv.	+	+	8	83	90
<i>Companion taxa</i>					
<i>Aulacomnium palustre</i>	13	17	.	.	60
<i>Erica tetralix</i>	37	+	.	.	10
<i>Carex arenaria</i>	50	100	17	+	.
<i>Quercus robur</i> juv.	.	.	8	25	10
<i>Calamagrostis epigeios</i>	.	.	33	+	10
<i>Scleropodium purum</i>	.	25	42	.	.
<i>Brachythecium rutabulum</i>	25	33	.	.	.
<i>Pohlia nutans</i>	.	.	.	8	50
<i>Dicranum scoparium</i>	37	8	.	8	.
<i>Salix arenaria</i>	.	.	.	.	70
<i>Parmelia physodes</i>	.	33	.	.	.
<i>Drepanocladus fluitans</i>	.	.	.	.	30
<i>Salix aurita</i>	.	.	.	.	20
<i>Juncus conglomeratus</i>	.	.	.	.	20

Occasional taxa
Pinus sylvestris juv. 2(8); *Populus tremula* juv. 3(8); *Trientalis europaea* 3(8); *Aulacomnium androgynum* 4(8); *Dryopteris spinulosa* 4(8); *Agrostis canina* 5(10); *Rhamnus frangula* 5(10); *Empetrum nigrum* 2(+); 5(+); *Cladonia arbuscula et mitis* 2(+); *Calluna vulgaris* 2(+); *Ptilium crista-castrensis* 2(+); *Alnus glutinosa* juv. 3(+); *Dryopteris austriaca* 4(+); *Calliergon stramineum* 5(+); *Potentilla erecta* 5(+); *Molinia coerulea* 5(+); *Drepanocladus uncinatus* 5(+).

Location of the stands

- Betula verrucosa* variant, Sh-1970-6, inland from the seaward dunes, adjacent to *Salici-Empetretum*, UC 64453435.
- Vaccinium vitis-idaea* variant, T8-1967-10, small depression, behind the second dune ridge, between the sea shore and the motorway, UC 74187065.
- Polytricho* - *Betuletum pubescentis*, Sh-1970-7 (Stand 3), the elongated depression, inland from the seaward dunes, VB 48753795.
- Carex nigra* variant, Sh-1967-8, the elongated depression, inland from the seaward dunes, VB 48043765.
- Eriophorum angustifolium* variant, Sh-1967-8, small wet depression, inland from the seaward dunes, VB 48453890.

Table XVIII. *Carex rostrata* - *Juncus effusus* community (1-3);
Carex nigra - *Calamagrostis epigeios* community (4)

Stand No	1	2	3	4
Number of samples	12	12	12	12
<i>Local C-combination Carex rostrata</i> - <i>Juncus effusus</i> community				
<i>Carex rostrata</i>	100 ⁵	17 ⁵	17 ⁵	.
<i>Juncus effusus</i>	33	75 ²	100 ⁵	.
<i>D-Carex nigra</i> variant				
<i>Carex nigra</i>	.	50 ²	50	25
<i>Betula pubescens</i> juv.	.	42	17	+
<i>Pohlia nutans</i>	.	8	25	.
<i>Local C-dominant Carex nigra</i> - <i>Calamagrostis epigeios</i> community				
<i>Calamagrostis epigeios</i>	.	33 ³	8	100 ⁵
<i>Companion taxa</i>				
<i>Quercus robur</i> juv.	.	8	.	33
<i>Melampyrum pratense</i>	.	8	.	25
<i>Betula verrucosa</i> juv.	.	.	8	.
<i>Populus tremula</i> juv.	.	.	.	17
<i>Alnus glutinosa</i> juv.	.	33 ⁴	+	8
<i>Juncus conglomeratus</i>	8	.	8	.
<i>Anthoxanthum odoratum</i>	.	8	8	.
<i>Deschampsia flexuosa</i>	.	+	.	8
<i>Salix arenaria</i>	.	.	17	.

Occasional taxa

Agrostis canina 1(8); *Sphagnum squarrosum* 1(8); *Dryopteris spinulosa* 2(8); *Drepanocladus fluitans* 3(8); *Polytrichum commune* 3(8); *Sphagnum recurvum* 3(8); *Carex arenaria* 4(8); *Dryopteris austriaca* 2(+); *Solanum dulcamara* 3(+).

Location of the stands

- Carex rostrata* sociation, Sh-1970-7, small wet depression, inland from the seaward dunes, VB 47733761.
- Carex nigra* variant, Sh-1967-8 (Stand 2), a wet part of the elongated depression, inland from the seaward dunes, VB 47993761. Sh-1970-7 (Stand 3), small wet depression, inland from the seaward dunes, VB 47713761.
- Carex nigra* - *Calamagrostis epigeios* community, Sh-1970-7, small depression inland from the seaward dunes, VB 47923765.

Table XIX. *Caricetum canescentis - nigrae* (1-3)

Stand No	1	2	3
Number of samples	12	12	11
<u>C-<i>Caricetum canescentis - nigrae</i></u>			
<i>Carex canescens</i>	100 ⁵	92 ²	36
<i>C. echinata</i>	+	.	.
<u>D-<i>Sphagnum recurvum</i> subass.</u>			
<i>Sphagnum recurvum</i>	8	100 ⁵	36 ²
<i>Drepanocladus fluitans</i>	.	92 ²	.
<i>Polytrichum commune</i>	.	50	9
<i>Calliergon stramineum</i>	.	17	.
<i>Calypogeia sphagnicola</i>	.	.	9
<u>D-<i>Calamagrostis canescens</i> variant</u>			
<i>Calamagrostis canescens</i>	.	.	100 ⁴
<i>Naumburgia thyrsiflora</i>	.	.	55
<i>Iris pseudacorus</i>	.	.	36
<u>C-<i>Caricion canescentis - nigrae</i></u>			
<i>Carex nigra</i>	67	25	64 ³
<i>Juncus filiformis</i>	.	.	27
<u>C-<i>Caricetalia nigrae</i> et <i>Parvocaricetalia</i></u>			
<i>Eriophorum angustifolium</i>	.	83	.
<i>Potentilla palustris</i>	.	.	44 ²
<i>Calliergon cordifolium</i>	.	.	27
<i>Drepanocladus exannulatus</i>	.	.	9
<i>Richardia pinguis</i>	.	.	9
<u>Companion taxa</u>			
<i>Juncus conglomeratus</i>	25	50	18
<i>Lysimachia vulgaris</i>	.	.	36
<i>Galium uliginosum</i>	.	.	36
<i>Lythrum salicaria</i>	.	.	36
<i>Juncus effusus</i>	.	58	.
<i>Betula pubescens</i> juv.	17	+	.
<i>Salix aurita</i>	.	33	.
<i>Myrica gale</i>	.	.	27
<i>Carex acuta</i>	.	.	18
<i>Salix arenaria</i>	.	17	.
<i>Aulacomnium palustre</i>	.	17	.

Occasional taxa

Pohlia nutans 1(8), 3(9); *Salix cinerea* 3(9); *Erica tetralix* 3(9); *Peucedanum palustre* 3(9); *Carex rostrata* 3(9); *Sphagnum squarrosum* 3(9); *Alnus glutinosa* juv. 1(8); *Drosera rotundifolia* 2(8); *Quercus robur* juv. 1(+); *Hydrocotyle vulgaris* 1(+); *Marchantia polymorpha* 1(+).

Location of the stands

- Carex canescens* sociation, Sh-1970-7, the elongated depression, inland from the seaward dunes, VB 48053768.
- 2-3 *Sphagnum recurvum* subass., Sh-1970-7 (Stand 2), small wet depression, inland from the seaward dunes, VB 48293778.
- 3 *Calamagrostis canescens* variant, T8-1965-6, the flat wide depression near a ditch, periodically inundated, UC 73957030.

Table XX. *Caricetum acutae* (1-4); *Sparganium minimum* community (5)

Stand No	1	2	3	4	5
Number of samples	12	12	11	10	12
<u>C-<i>Caricetum acutae</i></u>					
<i>Carex acuta</i>	100 ⁴	100 ⁵	91 ²	100 ³	8
<u>D-<i>Polygonum amphibium</i> subass.</u>					
<i>Polygonum amphibium</i>	8	75	.	.	42
<u>D-<i>Campylium polygamum</i> subass.</u>					
<i>Campylium polygamum</i>	8	.	100 ²	40	.
<i>Galium uliginosum</i>	.	8	73	50	.
<i>Calliergon cordifolium</i>	.	.	100	20	.
<u>C-<i>Magnocaricion</i> et <i>Magnocaricetalia</i></u>					
<i>Galium palustre</i>	25	.	.	50	.
<i>Scutellaria galericulata</i>	+	.	9	30	.
<i>Naumburgia thyrsiflora</i>	.	.	9	.	.
<i>Carex acutiformis</i>	+	.	.	.	.
<u>C-<i>Phragmitetia</i></u>					
<i>Iris pseudacorus</i>	.	17	27 ³	60 ²	.
<i>Phragmites communis</i>	8	+	100 ³	.	.
<i>Peucedanum palustre</i>	+	.	.	100 ³	.
<i>Lycopus europaeus</i>	.	+	9	20	.
<i>Alisma plantago-aquatica</i>	.	.	+	.	17
<u>Local C-<i>Sparganium minimum</i> community</u>					
<i>Sparganium minimum</i>	.	.	.	.	100 ⁵
<u>Companion taxa</u>					
<i>Lythrum salicaria</i>	25	42	36 ²	80 ²	8
<i>Lysimachia vulgaris</i>	67	.	55 ²	100 ⁴	.
<i>Cirsium palustre</i>	.	.	9	+	.
<i>Potentilla palustris</i>	25	92	+	30 ²	.
<i>Carex nigra</i>	.	25	100 ³	30 ²	.
<i>Agrostis canina</i>	.	.	9	10	.
<i>Drepanocladus exannulatus</i>	.	.	.	30	.
<i>Epilobium palustre</i>	.	.	.	20	.
<i>Carex canescens</i>	.	.	9	.	.
<i>Salix cinerea</i>	+	33 ²	+	20	+
<i>Carex rostrata</i>	17	.	.	.	.
<i>Veronica scutellata</i>	.	.	18	.	.

Occasional taxa

Viola canina 3(9); *Pellia epiphylla* 4(10); *Sphagnum recurvum* 4(10); *Juncus conglomeratus* 3(+), 4(+); *Phalaris arundinacea* 3(+), 4(+); *Equisetum palustre* 2(+); *Myrica gale* 2(+); *Salix arenaria* 3(+); *Juncus filiformis* 3(+); *Agrostis stolonifera* 3(+); *Rumex crispus* 3(+); *Betula pubescens* juv. 4(+).

Location of the stands

- 1-2 *Polygonum amphibium* subass., Sh-1970-7 (Stand 1), the elongated depression filled with water, between the seashore and the pond, UC 64583445. T8-1967-7 (Stand 2), the flat wide depression, inland from the seaward dunes, UC 73907045.
- 3-4 *Campylium polygamum* subass., T8-1965-6 (Stand 3), the flat wide depression, just behind the outer dunes, UC 73887025. T8-1971-10 (Stand 4), the flat wide depression, inland from the seaward dunes, near the ditch, UC 73957042.
- 5 *Sparganium minimum* community, Xh-1970-7, the elongated depression filled with water, between the seashore and the pond, UC 64583443.

Table XXI. *Ecological notes of the sites* (loss on ign. and pH are expressed as mean values)

Plant community; locality; soil profile	depth cm	loss on ign. %	pH		grain size (mm) %				number of samples
			H ₂ O	KCl	>2	2- 0.6	0.6- 0.2	<2	
Naked beach									
Ha-1967, 1971; beach syrosem, brown sand	0-10 50-60	0.24 0.58	7.2 8.7	6.4 8.1	- -	- 2.9	- 85	- 12	1 1
Tö-1966, 1967; beach syrosem, brown sand, several humus lenses, wet sand > 50 cm	0-10 50-60	0.17 0.20	7.2 7.1	6.3 6.7	- -	- 22	- 77	- 0.9	8 7
Fa-1972; beach syrosem, white sand	0-10	0.11	5.8	5.0	-	-	-	-	1
Sh-1966, 1967; beach syrosem, white sand, wet sand > 30 cm	0-10	0.14	6.8	6.2	-	-	-	-	9
Vm-1972; beach syrosem, white sand	0-10 50-60	0.14 0.14	6.9 8.5	6.6 7.6	- -	- -	- -	- -	1 1
Fb-1972; beach syrosem, white sand	0-10 50-60	0.10 0.13	6.2 7.0	5.7 6.3	- -	- -	- -	- -	1 1
Average naked beach	0-10 50-60	0.15 0.16	6.7 7.6	5.7 7.0	- -	- 8	- 80	- 12	6 5
Cakiletum maritima									
Tö-1966; beach syrosem mixed with seaweed, brown sand	0-10	0.49	6.4	6.1	-	-	-	-	1
Sh-1966, 1967; beach syrosem mixed with seaweed, white sand, few humus lenses, buried plant residues, wet sand > 50 cm	0-10 50-60	0.13 0.19	6.6 6.7	5.8 6.1	- -	- <0.1	- 78	- 22	8 7
Average Cakiletum maritima	0-10 50-60	0.31 0.19	6.5 6.7	5.8 6.1	- -	- -	- 78	- 22	2 1
Honkenyetum peploidis									
Tö-1966, 1967; beach syrosem with some seaweed, brown sand, several humus lenses, many rhizome parts, shells in the subsoil	0-10 50-60	0.22 0.19	7.0 7.2	6.4 6.5	- -	- 15	- 45	- 40	9 7
Åh-1972; beach syrosem, brown sand, shells throughout	0-10 50-60	0.23 0.34	7.0 7.6	6.5 7.2	- -	- -	- -	- -	1 1
Average Honkenyetum peploidis	0-10 50-60	0.23 0.27	7.0 7.4	6.5 6.9	- -	- 15	- 45	- 40	2 2
Honkenyo-Agropyretum acuti									
Fa-1972; syrosem mixed with seaweed, white sand, seaweed deposits at ca. 40 cm	0-5 50-60	0.26 0.65	6.6 7.5	5.7 7.1	- -	- -	- -	- -	1 1
Elymo-Ammophiletum typical subass.									
Ha-1967, 1971; dune syrosem, brown sand	0-10	0.32	5.8	5.1	-	0.2	79	21	1
Tö-1966, 1967; dune syrosem, brown sand, several humus lenses and root layers, rhizomes deeper than 100 cm	0-10 50-60	0.17 0.18	6.5 7.1	5.8 6.3	- -	- 0.1	- 96	- 4.1	16 7
Sh-1966, 1967; dune syrosem, white sand, few humus lenses, several root layers, rhizomes deeper than 100 cm, many buried shoots in the surface soil	0-10 50-60	0.13 0.16	6.2 6.4	5.4 5.7	- -	- <0.1	- 73	- 27	30 12
Average typical subass.	0-10 50-60	0.20 0.17	6.2 6.8	5.4 6.0	- -	- -	- -	- -	3 2
Hieracium umbellatum ssp. subass.									
Tö-1966, 1967; dune syrosem, brown sand, several humus lenses few root layers, many rhizomes throughout	0-10 50-60	0.26 0.18	5.6 6.6	4.4 5.3	- -	- 0.8	- 94	- 5.9	19 7
Sh-1966, 1967; dune syrosem, white sand, few humus lenses, several root layers, large rhizomes < 50 cm, small > 100 cm, a thin moss-layer in the surface	0-10 50-60	0.26 0.13	5.5 6.0	4.5 5.0	- -	- <0.1	- 59	- 41	26 7
Average Hieracium umbellatum ssp. subass.	0-10 50-60	0.26 0.16	5.6 6.3	4.5 5.2	- -	- 0.4	- 77	- 23	2 2
Cladonio (strictae)-Corynephorum									
Sh-1966, 1967; ranker-dune syrosem, A < 10 cm dark sand mixed with humus and small roots, few humus lenses, scattered roots < 50 cm, C > 10 cm yellowish white sand	0-10 50-60	0.51 0.10	4.8 5.6	3.8 4.4	- -	- <0.1	- 73	- 27	19 8
Fb-1972; ranker-dune syrosem, A < 20 cm grey sand mixed with humus and small roots, C > 20 cm light yellowish sand	0-10 50-60	0.49 0.21	5.1 5.5	3.8 4.7	- -	- 3	- 94	- 2.8	1 1
Average Cladonio-Corynephorum	0-10 50-60	0.50 0.16	4.9 5.6	3.8 4.6	- -	- 2	- 83	- 15	2 2
Violo-Corynephorum typical subass.									
Tö-1966, 1967; ranker-dune syrosem, brown sand mixed with humus in the surface soil	0-10	0.51	5.2	4.1	-	-	-	-	5
Cladonia subass.									
Tö-1966, 1967; ranker-dune syrosem, brown sand, A < 10 cm with dark humus, small roots < 15 cm, several humus lenses, scattered large roots, grey hard sand at ca. 100 cm	0-10 50-60	0.82 0.21	4.9 5.6	3.8 4.6	- -	- 5.9	- 91	- 3.0	13 7
Sh-1966, 1967; ranker-dune syrosem, white sand, A < 10 cm with dark humus, small roots < 15 cm, large roots < 30 cm, few humus lenses and root layers	0-10 50-60	0.55 0.16	5.1 5.9	4.0 5.0	- -	- <0.1	- 47	- 53	14 7
Vm-1972; ranker-dune syrosem, white sand	0-10 50-60	0.97 0.17	4.8 6.0	3.9 4.8	- -	- 1.3	- 95	- 3.9	1 1
Average Violo-Corynephorum	0-10 50-60	0.78 0.18	4.9 5.8	3.9 4.8	- -	- 2.4	- 78	- 20	3 3
Tortulo-Phleum arenarii									
Fa-1972; ranker-dune syrosem, white sand	0-5	1.4	5.5	5.9	-	-	-	-	1

Table XXI cont.

Plant community; locality; soil profile	depth cm	loss on ign. %	H ₂ O	pH KCl	grain size (mm)%				number of samples
					>2	2- 0.6	0.6- 0.2	<2	
<u>Teesdallo-Corynephorum typical subass.</u>									
Kevingehed-1972; podsol-ranker, A < 6 cm sand mixed with dark humus and roots, (B) 6-14 cm greyish sand, (B)-C > 14 cm brownish sand	0-10 50-60	1.3 0.66	4.6 4.9	3.9 4.3	- -	- -	- -	- -	1 1
Silvåkra-1972; ranker, A < 10 cm sand mixed with humus and roots, A-(B) 10-25 cm brownish sand, C > 25 cm yellowish sand	0-5 50-60	2.8 0.6	4.6 6.0	4.0 4.6	- -	- 0.1	- 43	- 57	1 1
Vomb-1972; ranker, A < 15 cm sand mixed with humus and roots (B)-C brownish sand	0-10 50-60	1.2 0.59	4.6 4.9	3.9 4.5	- <0.1	- 2.1	- 55	- 43	1 1
Vitaby-1972; podsol-ranker, strongly human influenced, A < 25 cm sand mixed with humus and roots, A-(B) 25-50 cm brownish sand, C > 50 cm yellowish sand	0-10 40-50 70-80	1.9 0.78 0.65	4.6 4.8 4.9	4.1 4.5 4.5	- 5.7 -	- 6.7 -	- 61 -	- 26 -	1 1 1
Average typical subass.	ca. 0-10 ca. 50-60	1.8 0.66	4.6 4.9	4.0 4.5	- 1.9	- 3.0	- 53	- 42	1 1
<u>Artemisia campestris subass.</u>									
Alstorp-1972; ranker, strongly human influenced, A < 19 cm sand with much humus, C > 19 cm brownish dry dirty sand also with roots	0-10 50-60	2.9 0.94	5.5 5.5	4.3 4.3	- 0.7	- 9.0	- 83	- 7.4	1 1
Silvåkra-1972; ranker, strongly human influenced, A < 15 cm dark sand mixed with humus and roots, C > 15 cm brownish sand	0-5 50-60	2.1 1.3	5.3 5.4	4.1 4.2	- 0.5	- 6.5	- 43	- 50	1 1
Björka-1972; ranker, A < 20 cm sand with much humus and roots, C > 20 cm yellowish sand	0-10 50-60	1.3 0.52	5.1 6.4	4.3 5.0	- <0.1	- 2.3	- 76	- 21	1 1
Average Artemisia campestris subass.	ca. 0-10 50-60	2.1 0.92	5.3 5.8	4.3 4.5	- 0.4	- 5.9	- 69	- 26	3 3
<u>Pleurozium schreberi-Agrostis tenuis comm.</u>									
Åh-1972; ranker, a layer of humus and roots in the surface, brownish sand	0-5	2.7	3.9	3.5	-	-	-	-	1
<u>Thero-Airion communities (of other kind)</u>									
Fa-1972 (Armeria maritima var. elongata); ranker (?)	0-5	4.5	5.1	4.1	-	-	-	-	1
Fa-1972 (Aira praecox) ranker (?)	0-5	2.2	4.2	3.3	-	-	-	-	1
Fa-1972 (Festuca ovina) ranker (?)	0-5 50-60	2.9 0.32	4.6 5.3	3.5 4.4	- -	- -	- -	- -	1 1
Björka-1972 (Festuca ovina); podsol-ranker, A < 23 cm sand mixed with dark humus, roots < 5 cm, (B)-C > 23 cm brownish sand	0-10 50-60	1.7 1.1	5.2 5.9	4.0 4.6	- -	- -	- -	- -	1 1
<u>Antherico-Koelerietum glaucae</u>									
Vm-1972; pararendzina, sand mixed with humus in the surface	0-10	-	8.4	7.6	-	-	-	-	1
soil, C > 40 cm coarse calcareous glacialfluvial soil	40-50	-	9.2	8.5	-	-	-	-	1
<u>Salicetum arenariae</u>									
<u>Humophilla arenaria subass.</u>									
Hä-1967; dune syrosem, brown sand, leaf litter and scattered mosses on the surface	0-10	0.59	-	-	-	-	-	-	1
Tö-1966, 1967; dune syrosem, brown sand, leaf litter and scattered mosses on the surface, few root layers, some big roots > 100 cm	0-10 50-60	0.64 0.20	6.0 6.3	4.8 4.8	- -	- 4.5	- 94	- 1.6	7 7
<u>Carex nigra subass.</u>									
Tö-1966, 1967; ranker, moist brown soil, thin humus layer in the surface soil, small roots < 15 cm, big roots < 40 cm, water table > 60 cm	0-10 50-60	1.9 0.22	5.5 5.3	4.4 4.4	- -	- -	- -	- -	7 2
<u>Salici-Empetretum</u>									
<u>Festuca arenaria subass.</u>									
Tö-1966, 1967; ranker-dune syrosem, brown sand, irregular humus zones and lenses < 50 cm, roots and root layers mainly < 50 cm	0-10 50-60	0.49 0.39	5.4 5.5	4.1 4.2	- -	- 0.2	- 40	- 60	9 7
<u>Polypodium vulgare subass.</u>									
Fa-1972; ranker, raw humus < 2 cm, A 2-6 cm sand mixed with humus, C > 6 cm white yellowish sand	0-5 0-10 50-60	3.7 0.93 0.10	4.7 4.8 6.6	3.3 3.6 6.3	- - -	- - 0.6	- - 95	- - 5	1 1 1
Sh-1966, 1967; ranker, raw humus < 4 cm, A 4-12 cm sand mixed with humus, C > 12 cm yellowish sand, roots mainly < 20 cm	0-10 50-60	1.4 0.19	4.4 5.7	3.4 4.7	- -	- <0.1	- 49	- 51	16 7
Average Polypodium vulgare subass.	0-10 50-60	1.2 0.15	4.6 5.7	3.5 4.7	- -	- 0.3	- 72	- 28	2 2
<u>Lophocolea heterophylla subass.</u>									
Hä-1972; ranker, raw humus < 5 cm, A 5-12 cm sand mixed with humus, C > 12 cm yellowish coarse sand with rusty mottling	0-10	4.1	-	-	-	-	-	-	1
Tö-1966, 1967; ranker, raw humus < 3 cm, A 3-20 cm sand mixed with humus, C > 20 cm brownish sand, roots < 35 cm, moist sand > ca. 100 cm	0-10 50-60	2.7 0.24	4.7 6.2	3.6 4.8	- -	- 3.4	- 60	- 37	13 6
Åh-1972; ranker, raw humus < 6 cm, A 6-15 cm sand mixed with humus, C > 15 cm yellowish sand	0-5 0-10 50-60	5.6 3.5 0.24	4.4 4.2 5.5	3.2 3.2 4.4	- - -	- - 0.6	- - 99	- - 0.2	1 1 1
Sh-1966, 1967; ranker, raw humus < 5 cm, A 5-15 cm sand mixed with humus, C > 15 cm yellowish white sand	0-10	2.6	4.4	3.7	-	-	-	-	7
Average Lophocolea heterophylla subass.	0-10 50-60	3.2 0.24	4.4 5.9	3.4 4.6	- -	- 2.0	- 80	- 18	3 2
<u>Genistio-Callunetum (moraine reference)</u>									
Mästocka-1972; podsol, raw humus (O+A) < 3 cm, E 3-15 cm, B 15-40 cm, C > 40 cm	0-3 3-15 15-40 >40	33 6.0 8.5 1.6	4.4 4.7 5.0 5.2	3.2 3.3 4.3 4.5	- - - -	- - - -	- - - -	- - - -	1 1 1 1

Table XXI cont.

Plant community; locality; soil profile	depth cm	loss on ign. %	H ₂ O	pH KCl	grain size (mm)% >2 2-0.6 0.6-0.2 <2	number of samples
<i>Calluna vulgaris</i> soc.						
Sh-1967, 1971; podsol, raw humus < 3 cm, A 3-28 cm sand mixed with humus, B 28-136 cm sand with rusty mottling, C > 136 cm yellowish white sand	0-10 20-30 50-60 140-150	4.7 0.68 0.93 -	4.3 4.8 4.9 5.1	3.3 3.7 4.2 4.5	- - - -	5 2 1 1
Revingehed-1972; podsol, raw humus < 5 cm, A 5-25 cm sand mixed with humus, B-C > 25 cm mineral soil with rusty mottling	0-5 0-10 50-60	5.7 2.7 0.68	5.2 4.9 5.1	4.3 3.8 4.3	- - -	1 1 1
Average <i>Calluna vulgaris</i> soc.	0-10 50-60	3.7 0.80	4.6 5.0	3.5 4.2	- - -	2 2
<i>Agrostio-Callunetum</i>						
Björka-1972; podsol-ranker, raw humus < 1 cm, A 1-25 cm sand mixed with humus, roots < 5 cm, (B)-C > 25 cm brownish mineral soil, coarse sand and gravel > 50 cm	0-10 50-60	2.4 1.0	5.0 5.1	3.9 4.4	- - -	1 1
Hemmetorp-1972; podsol-ranker, raw humus < 2 cm, A 2-25 cm sand mixed with humus, (B)-C > 25 cm coarse brownish mineral soil	0-5 50-60	3.1 1.2	4.5 4.7	3.5 4.3	- - -	1 1
Vitaby-1972; podsol-ranker, strongly human influenced A < 55 cm sand mixed with humus and roots, (B)-C > 55 cm brownish mineral soil	0-5 0-10 60-70	3.1 3.5 1.9	4.5 4.6 4.9	3.7 3.7 4.3	- - -	1 1 1
Average <i>Agrostio-Callunetum</i>	ca. 0-10 ca. 50-60	3.0 1.3	4.7 4.9	3.7 4.3	- - -	3 3
<i>Molinio-Myricetum gale</i>						
<i>Salix arenaria</i> subass.						
Ha-1967, 1971; ranker, moist sand mixed with humus in the surface soil	0-5 0-10	5.0 2.3	4.8 4.7	3.9 3.9	- - -	1 1
Tö-1966, 1967; ranker, moist sand mixed with humus in the surface soil	0-10	3.8	5.4	4.6	- - -	7
Average <i>Salix arenaria</i> subass.	0-10	3.1	5.0	4.2	- - -	2
<i>Cladonio-Pinetum sylvestris</i>						
<i>Corynephorus canescens</i> subass.						
Tö-1967; podsol-ranker	0-5 0-10	1.4 0.90	- -	- -	- - -	1 1
<i>Vaccinio-Pinetum sylvestris</i>						
<i>Empetrum nigrum</i> subass.						
Ha-1971; podsol, raw humus with roots (O+A) < 2 cm, E 2-12 cm, B 12-55 cm, C > 55 cm	0-5 0-10 50-60	4.5 3.5 0.67	4.5 4.1 4.9	3.8 3.4 4.6	- - - 22 41 37 0.3	1 1 1
Tö-1967; podsol	0-5 0-10	9.6 3.4	- -	- -	- - -	1 1
<i>Quercus petraea</i> subass.						
Ha-1971; podsol, raw humus (O+A) < 9 cm, E 9-15 cm, B 15-46 cm, C > 46 cm	0-5 0-10 50-60	25 11 0.75	4.1 4.0 4.7	3.0 3.1 4.4	- - - 3.3 87 11	1 1 1
Typical subass. (moraine reference)						
Lidhult-1972; podsol, raw humus (O+A) < 7 cm, E 7-18 cm, B 18-98 cm, C > 98 cm	0-7 7-18 25-30 70-80	87 1.7 3.3 1.0	4.1 4.5 4.6 5.1	2.8 3.2 3.9 4.0	- - -	1 1 1 1
<i>Deschampsia flexuosa</i> - <i>Pinus sylvestris</i> comm.						
Sh-1970, 1971; podsol, raw humus < 8 cm, A 8-17 cm sand mixed with humus, B 17-44 cm, second A 44-72 cm, second B 72-120 cm, C > 120 cm	0-5 50-60 100-110 190-200	55 2.4 - -	3.9 4.0 4.7 4.9	2.9 3.2 4.3 4.2	- - -	2 1 1 1
Fb-1972; podsol, raw humus < 8 cm, A 8-23 cm sand mixed with humus, B 23-100 cm reddish sand mottled with humus, C > 100 cm (about)	0-5 0-10 50-60 100-110	14 2.5 0.27 0.21	4.0 4.1 5.1 5.5	2.9 3.0 4.1 4.5	- - -	1 1 1 1
<i>Pseudopinetum sylvestris</i>						
Vm-1972; podsoloid, strongly influenced by man, coarse brownish sand, on a pararendzina	50-60	0.18	7.5	6.0	- - -	1
Revingehed-1972; podsol, influenced by man, raw humus < 6 cm, E 6-8 cm.	0-10 50-60	2.9 1.4	4.7 4.7	3.8 4.2	- - -	1 1
<i>Oxalis acetosella</i> - <i>Quercus petraea</i> comm.						
Ha-1971; podsoloid, raw humus < 5 cm, A < 23 cm sand mixed with humus, B+C > 23 cm	0-5 0-10 50-60	12 9.5 0.63	4.7 4.5 5.1	3.8 3.7 4.1	- - - 2.3 84 13	1 1 1
(Ha-1971, on the old dunes)	0-5 0-10	9.3 5.3	5.1 4.8	4.2 4.0	- - -	1 1

Table XXI cont.

Plant community; locality; soil profile	depth cm	loss on ign. %	pH		grain size (mm) %				number of samples
			H ₂ O	KCl	>2	2- 0.6	0.6- 0.2	<2	
<u>Melampyro-Quercetum roboris Calamagrostis epigeios vicariant</u> <u>typical subass.</u>									
Sh-1967, 1970, 1972; <i>Luzula campestris</i> var., podsol, raw hu- mus < 6 cm, A 6-11 cm sand mixed with humus, B 11-73 cm, second A 73-96 cm, second B 96-162 cm, C > 162 cm	surface 40-50 80-90 150-160 240-250	8.7-80 - 2.0 - -	4.1 4.9 4.9 5.0 5.5	3.2 4.0 4.0 4.0 4.6	- - - - -	- - - - -	- - - - -	- - - - -	16 1 2 2 2
Sh-1970, 1972; <i>Vaccinium myrtillus</i> var., podsol, raw humus (0+A) < 15 cm with big roots, B+C > 15 cm reddish brown sand	0-5 0-10 50-60	45 39 1.1	4.2 4.1 4.6	3.1 3.0 3.7	- - -	- - 1.2	- - 93	- - 6.0	1 2 1
Sn-1970, 1972; <i>Pteridium aquilinum</i> var., podsol, raw humus < 5 cm with roots, A 5-25 cm sand mixed with black humus, B+C > 25 cm hard reddish mottled sand also with humus, pan at about 50 cm, sea gravels > 160 cm	0-5 0-10 50-60	64 15 -	4.2 4.0 4.5	3.2 3.1 3.8	- - -	- - -	- - -	- - -	1 2 1
Average typical subass.	surface ca. 50-60	34 1.1	4.1 4.6	3.1 3.8	- -	- 1.2	- 93	- 6.0	5 3
<u>Corylus avellana subass.</u>									
Sn-1970; podsoloid (?)	surface	9.4	4.1	3.2	-	-	-	-	4
<u>Corynephorus canescens subass.</u>									
Sh-1970; podsol-ranker (?)	surface	0.45	4.9	3.9	-	-	-	-	2
<u>Melampyro-Quercetum roboris inland vicariant</u>									
Xn-1972; podsol, raw humus < 9 cm, A < 20 cm sand mixed with humus, B+C > 20 cm weakly reddish brown sand	0-5 0-10 50-60	5.8 2.6 0.40	4.5 4.6 5.2	3.8 3.5 4.4	- - -	- - -	- - -	- - -	1 1 1
Tönnersjö-1972; (reference on moraine), podsol, raw humus < 7 cm, E 7-15 cm, B 15-82 cm, C > 82 cm (see Fig. X).	0-5 5-7 7-15 15-82 >82	86 52 5.9 4.9 1.2	4.5 4.2 4.3 4.8 5.1	3.4 3.1 3.2 4.3 4.2	- - - - -	- - - - -	- - - - -	- - - - -	1 1 1 1 1
<u>Agrostio-Quercetum roboris</u>									
Sn-1970; podsoloid (?)	surface	2.9	5.1	4.4	-	-	-	-	2
Revingehed-1972; podsoloid, A < 10 cm, sand mixed with humus and roots, (B) 10-25 cm weakly reddish mineral sand, C > 25 cm white yellowish sand	0-5 0-10 50-60	5.7 2.7 0.68	5.2 4.9 5.1	4.3 3.8 4.8	- - -	- - -	- - -	- - -	1 1 1
Hemnestorr-1972; podsol, raw humus < 4 cm, A sand rust coloured and humus mottled < 22 cm, B+C > 22 cm, scattered roots > 50 cm	0-5 0-10 50-60	8.1 3.6 1.7	4.2 4.3 4.6	3.2 3.3 4.2	- - 2.5	- - 12	- - 71	- - 15	1 1 1
Average Agrostio-Quercetum roboris	surface 50-60	4.6 1.2	4.7 4.9	3.8 4.2	- 2.5	- 12	- 71	- 15	5 2
<u>Irido-Alnetum glutinosae</u>									
<u>Pinum punctatum subass.</u>									
T8-1967, 1971; aue soil, A < 10 cm black highly decomposed humus layer, brownish sand saturated with water > 10 cm	0-5 0-10 20-30	50 48 -	5.5 5.7 -	5.0 5.2 -	- - 3.6	- - 9.9	- - 87	- - -	1 1 1
Xn-1972; aue soil, A black highly decomposed humus layer	0-5 0-10	30 21	6.4 6.4	5.2 5.6	- -	- -	- -	- -	1 1
Average Irido-Alnetum glutinosae	0-10 20-30	35 -	6.1 -	5.4 -	- 3.6	- 9.9	- 87	- -	1 1
<u>Athyrio-Alnetum glutinosae</u>									
T8-1971; hydromorphous soil or moist podsol, A < 15 cm peaty raw humus, reddish brown mineral sand > 15 cm, water > 40 cm	0-5 0-10	66 56	4.3 4.2	3.5 3.6	- -	- -	- -	- -	1 1
<u>Filipendulo-Alnetum glutinosae</u>									
T8-1971; pseudogley, sandy mill < 20 cm, dark sand mixed with humus < 35 cm, S 35-55 cm brown sand with rusty mottling, C > 55 cm also with water	0-5 0-10	16 20	5.0 5.1	4.5 4.4	- -	- -	- -	- -	1 1
<u>Myrico-Betuletum pubescentis</u>									
T8-1967; hydromorphous soil or moist podsol	0-5 0-10	13 4.9	- -	- -	- -	- -	- -	- -	1 1
<u>Polytricho-Betuletum pubescentis</u>									
Sh-1967; fen armour soil or fen peat soil, the brownish humus is irregularly decomposed lying directly on the sand	0-10 40-50	8.7 -	4.2 5.2	3.5 4.6	- -	- -	- -	- -	5 1
<u>Carex rostrata-Juncus effusus comm.</u>									
Sh-1967; fen peat soil or fen armour soil, dark highly de- composed humus lying directly on the sand	0-10	35	4.9	3.9	-	-	-	-	2
<u>Caricetum canescentis-nigrae</u>									
T8-1966, 1967; fen armour soil or fen peat soil, the brownish humus is irregularly decomposed lying directly on the sand	0-10	5.9	5.1	4.3	-	-	-	-	4
<u>Caricetum acutae</u>									
<u>Polygonum amphibium subass.</u>									
T8-1967; hydromorphous soil, aue or armour, black highly de- composed though humus lying directly on the sand	0-10	27	4.9	4.4	-	-	-	-	1
<u>Campylium polygamum subass.</u>									
T8-1966, 1967; hydromorphous soil, fen armour soil (?), ir- regularly decomposed humus lying directly on the sand	0-10	4.0	5.6	4.5	-	-	-	-	4

Table XXII. Pollen and spore frequency (%) at various depths (cm) in the sand at Sandhammaren.

Pollen or spore type	Melampyro - Quercetum roboris Luzula camp. var.			Deschampsia flexuosa - Pinus sylvestris comm.			Polytricho - Betuletum pub. Carex nigra var.		
	0-5	115-110	150-155	0-5	31-36	50-55	100-105	0-5(1)	0-5(2)
Salix	1	1	5	17	<1	-	7	<1	<1
Betula	6	37	31	8	33	20	9	19	23
Pinus	8	9	23	55	9	24	63	6	4
Alnus	<1	48	31	18	51	51	17	74	71
Quercus	85	2	3	3	6	2	4	1	<1
Corylus	-	13	7	3	26	32	4	-	-
Fagus	-	1	4	-	1	-	-	-	<1
Carpinus	-	1	3	-	-	-	-	-	<1
Picea	-	<1	<1	-	-	-	-	-	-
Calluna	3	180	130	310	660	59	34	4	1
Wild grasses	5	3	3	5	2	10	36	3	1
Umbelliflorae	<1	<1	2	17	<1	-	2	<1	-
Artemisia	-	2	1	10	<1	23	7	1	<1
Liguliflorae	-	<1	1	5	<1	3	2	-	<1
Sphagnum	-	<1	1	-	4	-	-	-	-
Tubuliflorae	-	-	-	2	<1	<1	-	<1	<1
Ferns	-	-	-	-	1	-	<1	3	21

